

# HULL BULLETINS OF MARINE ECOLOGY

VOLUME III

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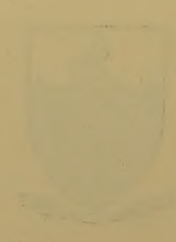
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VOLUME III

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# LIST OF PERSONNEL OF THE DEPARTMENT OF OCEANOGRAPHY, UNIVERSITY COLLEGE OF HULL. 1941-1950.

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(In 1948 Dr. Lucas was appointed Director of Fisheries Research, Scottish Home Department, and Mr. K. M. Rae became the acting Head of the Department.)

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(Acting Head of the Department, 1948-1950.)

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*N. B. Marshall*, M.A.(Cantab.), 1937-1947.

C. B. REES, D.Sc.(Wales), 1937-

*H. G. Stubbings*, M.A., Ph.D.(Cantab.), B.Sc.(London), 1939-1946.

R. S. GLOVER, B.Sc.(Manchester), 1945-

*A. Saville*, B.Sc.(Aberdeen), 1946-1948.

F. R. VANE, M.Sc.(Liverpool), 1947-

*H. R. Schurr*, B.Sc.(Glasgow), 1949-1951.

*Experimental Officers :*

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G. A. COOPER, 1947-

Miss M. F. JOBSON, B.Sc.(St. Andrews), 1947-

Miss D. E. JOHN, 1947-

*Miss D. E. Williams* (Mrs. A. Saville), B.Sc.(Wales), 1947-1948.

*Laboratory Stewards :*

J. SCRIVENER, 1935-

*F. H. Dewing*, 1937-1949.

*Names in italics indicate those members who have left the Department.*



## EXPLANATION

*A non-technical account of the contents of Volume III by the Editors*

THESE accounts of marine ecological researches, being essentially contributions to the scientific literature of this particular field of oceanography, are apt to be too specialized to be readily understood by the general reader. When the series was begun as a publication of the University College of Hull to report the work of its Department of Oceanography, it was decided to preface each volume with a brief non-technical account of its contents so that those of the general public, and particularly the members of the fishing industry, who were interested in the development of this branch of science, could have some indication of the progress being made. The present volume, the third, is the last to be published by the College, now the University of Hull, and in future the series will be continued as *The Bulletins of Marine Ecology* published by the Scottish Marine Biological Association at their Oceanographic Laboratory at Edinburgh; this change itself requires some explanation which may well be given here.

The beginnings of the work at Hull are fully described in the *Explanation* of Volume I which is also an introduction to marine ecology in general. This should be consulted by those who are not familiar with these investigations; here we will only remind the reader of their general nature. They began in 1932 with the introduction of a new method of surveying the plankton, the small drifting life of the sea, which is so important in relation to the fisheries as the basic food supply of all other marine life. The distribution of the plankton organisms of many different kinds and their relative abundance are continually varying. The main object of these investigations is to study the major changes taking place in the plankton month by month over a wide area so that eventually it may be possible to have a better understanding of the fluctuations in the fortunes of the fisheries; it is believed that these fluctuations must, at least in part, be affected by the changes in the plankton or in the variations in the flow of ocean currents which may be so well indicated by them. Such a study of the continual changing plankton over a vast area of sea cannot be undertaken by a single research ship. The essential feature of the new method is the use of a number of automatic plankton-sampling machines, the continuous plankton recorders, which can be towed behind commercial steamships along their different routes across the sea and so sample mile by mile the changing nature of the plankton at a standard depth of 10 metres.

From 1932 to 1937 the survey was confined for a trial period to the southern North Sea on lines radiating from Hull to the continent. The results of this first five years experiment were so promising that in 1938 a new Laboratory was opened in Leith to operate more northern lines so that the whole of the North Sea was covered every month by a network of observation. Then came the war which



inevitably made a complete break in the work. Fortunately the results of 1938 and the first half of 1939 had given a good demonstration of the value of the larger survey in indicating the extent of the influx of Atlantic water month by month into the North Sea. The work was taken up again in 1946 and began to expand still further with the important assistance of the weather ships in carrying the recorder lines out into the Atlantic. Professor Hardy, who had founded the survey in 1932, had left in 1942 to become the Regius Professor of Natural History at Aberdeen and later Linacre Professor at Oxford, although he continued to be the Honorary Director of the survey until 1950; Dr. C. E. Lucas, who followed him as Head of the Department of Oceanography (now separated from that of Zoology) was in 1948 appointed Director of Fisheries Research to the Scottish Home Department and in turn was succeeded by Mr. K. M. Rae. The work which had begun as a piece of university research in the development of new methods of plankton survey was now passing beyond the initial pioneer stage to become a long term project with the centre of operations no longer based upon the southern North Sea. These three features—the change in the scope of the work, the shift in its geographical centre and the departure of its initiator from the College—all indicated that a change in the organization of the investigations was due. In 1950 the Development Commissioners who have from the beginning so generously supported these researches, recommended that the work should be transferred to a separate institute at Edinburgh to become a second laboratory of the Scottish Marine Biological Association. The former premises at Leith were no longer large enough to accommodate the whole department and a suitable house at 78 Craighall Road was bought and very well converted into the new Oceanographic Laboratory which is now its home.

Since this is the last volume to be published under the old title of *Hull Bulletins of Marine Ecology* the editors, who have been associated with the work from its early days, would like to take this opportunity of expressing their gratitude to the Council and Senate of the University College of Hull for their encouragement and support which made the beginnings possible. Without that support this new venture in oceanography would never have been born.

We will now give a brief outline of the contents of the volume. The first paper, Bulletin No. 17, by Dr. Lucas and Mr. Rae, is a study of the changing water conditions in the southern North Sea from 1930 to 1937, as indicated mainly by the records of salinity (the varying degrees of saltiness) of the surface waters obtained on a number of steamship routes, under the organisation of the Conseil Permanent International pour l'Exploration de la Mer and published in their *Bulletins Hydrographiques*. By drawing the results along the different lines as graphs and appropriate symbols, trends in the changes of salinity are indicated which could not have been realised from the data in their original form and so a new picture of the hydrological background to the changing plankton distribution is obtained. This study reveals a gradual increase in the salinity of the surface waters of the central and southern North Sea and English Channel from 1932 to reach a maximum in the winter of 1934–5 followed by an equally marked decline. While there is evidence that the



increase in the central North Sea must have been derived largely from the northern Atlantic influence, that in the Southern Bight and English Channel must be due to the influx from the southwest. Among other striking features brought out by this new treatment of the data is a demonstration of the occasional passage of large patches of unusually low salinity water up the Channel into the southern North Sea.

The next Bulletin, No. 18, is not directly concerned with the plankton recorder survey but is a record of observations made on the food and feeding habits of trawl-caught fish: principally cod at Bear Island, and in addition some information regarding cod and haddock off Iceland and the Murman coast. Mr. W. W. Brown, when a research student from Leeds University working at the Hull department, began a study of the food of the cod at Bear Island; in addition to making voyages on trawlers to collect material he organised a system of collecting preserved stomachs on a number of trawlers whose skippers kindly co-operated in the work. Similar material from Iceland and the Murman coast was obtained by other students making voyages and incorporated in the present study. The analysis of the material which was begun by Mr. Brown was completed by Dr. C. Cheng, a Chinese research student working at the department. The results from Bear Island show a marked seasonal change in the food of the cod from a diet in which pelagic crustacea, particularly euphausiids. Amphipods and carid prawns form a large part in the spring and summer to one in the autumn and winter in which the herring becomes more important. The capelin may also at times be taken in large numbers in the summer. The samples from Iceland and the Murman coast are relatively small in number and their main interest is in the comparison of the food taken on the same grounds at the same time by the two closely related species: cod and haddock. The haddock seem to be feeding mainly on various invertebrate animals on the sea bed: worms, molluscs, sea-urchins and brittle-stars, and not at all on fish except for a few sand eels; the cod, while taking some invertebrates (particularly brittle-stars and prawns), is mainly feeding upon fish: herring, capelin, codling and sand eels. The two species can occupy the same grounds without coming into serious competition with one another for food.

In the next two Bulletins, Nos. 19 and 20, Dr. C. B. Rees makes a study of the planktonic larval stages of the bottom-living bivalve molluscs, lamellibranchs such as the mussel which are so important as the food of trawl-caught fish, particularly of the plaice in the North Sea. In the first paper he makes a detailed study of the many different kinds of larvae and evolves a new system for their identification based upon the shape and texture of their shells and particularly upon the differences in the form of the hinges between the paired valves; the paper is extensively illustrated with plates of photographs and text figures to enable the identifications to be made by other workers. Altogether he describes seventy-seven different types of such larvae in the North Sea. This intricate and painstaking research forms an essential preliminary step leading to the recognition of the different kinds encountered on the plankton recorder rolls and so to the study of their seasonal distribution over the North Sea which is described in the next paper, Bulletin No. 20.



The month by month distribution of the different species are here shown in a series of plates and text figures. The occurrence of dense swarms of larvae in the same places in different years and the sequence of species from month to month suggest a definite pattern of distribution. Some of the patches of larvae can be related to recognised eddy swirls in the North Sea current system. The greatest number of species occurred in October with a secondary maximum in June. The majority of species appear to have only one main breeding season in the year, but a few have two distinct periods. Rough estimates of the duration of pelagic life and the speed of water movements show that larvae may be transported for considerable distances in the North Sea from the positions at which they were liberated to where they finally settle down.

Bulletin No. 21 is an account by Mr. Rae of the revival of the plankton recorder survey after the war and its development in the years 1946 to 1949. This, which itself is an explanation of the changes in the plan of the survey and of certain modifications made in the methods of working up the results, requires little further explanation here. There is a list of all the records taken during this period and a series of charts showing the area covered in each month. An appendix gives a detailed account of the methods of analysis applied to plankton of different categories on the recorder rolls as at present practised.

In Bulletin 22 Dr. Rees takes up the study of another group of planktonic larvae of the bottom-living invertebrate fauna, those of the decapod crustaceans which include the crab, lobster, shrimp and prawn-like animals. These larvae on the whole occur in much larger numbers in the more southern part of the North Sea than in the north. The period of greatest abundance is July to August with a smaller peak in April to May. He gives the distributions and seasons of 41 species; the areas in which they are found in the plankton agree well with the known distribution of the adults. An interesting fact has emerged that some species which are in general known to be more northerly in distribution appear to breed more successfully in the south of the North Sea than in its more northern part, and *vice versa* for more southern species; this is explained by the lower temperature of the bottom water in the southern North Sea in winter.

In the next paper, No. 23, Mr. R. S. Glover deals with the distribution (as shown by the plankton recorder) of those planktonic prawn-like crustacea of the Order Euphausiacea which are not only important as fish food but often so valuable as indicators of water movements. Apart from one rarity there are seven species which are well represented in the area of the survey and they fall into three categories. Two are oceanic species which only occur in the upper layers over water of more than 500 fathoms depth out to the west of the continental slope. Two others are also oceanic species but may be found over a wide range of depths: over the continental shelf and as far out into the Atlantic as our survey has gone. Then there are three more shallow water species. Of these one is mainly found in the region of the Skagerrak and probably represents a resident population without recruitment from the Atlantic; the other two have a distribution and movement



in the North Sea which closely corresponds to that of some other plankton species (certain copepods, pteropods and the arrow-worm *Sagitta elegans*) which are characteristic of the mixed coastal and oceanic water and are seen to progress down the western side of the North Sea. The main origin of one of these species is shown to lie over the continental slope in the Atlantic where its major spawning takes place.

The last Bulletin of the volume, No. 24, by Dr. Henderson is a particularly important one because it brings together all the records of young fish and fish eggs for the period 1932-39, as well as those for 1946-49. Work on the data for the pre-war period was begun by Dr. H. G. Stubbings, who, through the break caused by the war, was unable to finish the work before taking up another appointment; he had, however, prepared the main charts of distribution for this 1932-39 period and these, together with a short explanatory text, were published in 1951 as Bulletin No. 15 (in Volume II). This set of charts must be used in conjunction with the present paper. For the charts of distribution the material is plotted in the following groups: total fish eggs, total young fish excluding the Clupeidae (the herring family), the Clupeidae, the Ammodytidae (the sand-eel family), the Gadidae (the cod family) and the Pleuronectidae (the flat-fish). In the earlier part of the survey it was not possible to identify to species more than a very small part of the material; with an improvement made in the recorder to reduce the crushing of the specimens as they are passed through the mechanism and a re-arrangement of the work to allow the material to be examined soon after being collected, it has been possible to identify a high proportion of the young fish in selected samples. On such charts the predominating species are shown by various reference letters. It will be unnecessary here to repeat the main findings which are given in non-technical terms in the summary to this paper on pages 248-250, but attention may be drawn to one most striking result. On page 241 two graphs are shown together: one represents the number of fish eggs taken by the plankton recorder in the southern North Sea for each of the years 1932 to 1939 and from 1946 to 1949 and the other shows for the same years the average catch per 100 hours fishing of trawlers landing at British ports from the same area. The correspondence between the two graphs is quite remarkable; the more so because it is the eggs of *all* fish which are compared with the landings of only those fish of commercial value. This might suggest that the numbers of both commercial and non-commercial fish fluctuate together or that common factors influence their abundance. But a more likely explanation may lie in the fact that by far the majority of the fish eggs found in the plankton belong to the commercial species and so reflect closely the total population of mature individuals of those species in the manner first postulated many years ago by the German scientist Hensen. However, in either case we may assume that the total number of fish eggs in the plankton can give a sound idea of the quantity of catchable fish available. Further interesting comparison is made between the numbers of young fish taken by the recorder and those found over the same periods in the regular townnettings taken in the Channel off Plymouth; it shows the existence of very different trends in the two areas.





# THE PLANKTON OF THE NORTH SEA IN RELATION TO ITS ENVIRONMENT

## PART I.—THE HYDROLOGICAL BACKGROUND IN THE SOUTHERN NORTH SEA, 1930-37

BY

C. E. LUCAS, D.Sc., AND K. M. RAE, O.B.E., B.Sc.

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### INTRODUCTION.

ACCOUNTS of the Continuous Plankton Recorder surveys in the Southern North Sea, 1932-37, have been given by Hardy (1939), Lucas (1940), Rae and Fraser (1941), Henderson and Marshall (1944), and Stubbings (in the press). No detailed attention was paid in these to the relations between the plankton and its environment, largely because of the absence of immediately relevant material. The data reviewed here provides a partial hydrological background against which changes in the plankton may be seen; since they are fairly extensive, it seems best to consider them first separately and then (in Part II) in relation to the plankton. This, in turn, may reflect further light on the water movements during the period and some aspects of the data will be considered further in that part.

At this late date it might seem suitable also to review the data for 1938 and 1939, but some of them are not yet available, although reference will be made to certain aspects which are known to be relevant.

In the absence of any *ad hoc* material for correlation with the plankton records, it is necessary to make such use as we can of material taken with other objects in view. The normal methods of hydrological survey are generally unsuitable for comparison with data which are essentially continuous in space, and which are taken over the same routes for much longer periods than usual. The typical hydrological cruise involves a set of stations over a particular area, stations at least twenty miles apart and extending over a period of several days. The next cruise in such an area is likely to be at least three months later, and may well be more than a year after the first. More suitable material is found in the routine samples at stations on regular steamship lines and from light-vessels. Although only one of these steamship lines coincides with a plankton recorder route, there is a set of them crossing the Southern North Sea which provides regular standards for comparison. Against the limitation that the material has been collected only at the surface, and that the observations are limited to temperatures and salinities, are set the advantages of regularity and consequent standardization. In so far as continuity in space has been a feature of the recorder work, it would be most desirable to have similar continuity in hydrological data for comparison. Unfortunately, however, the only continuous physical data, certain thermographs, are confined mainly to the Northern North Sea.<sup>1</sup>

The routine observations mentioned, *bateaux routiers* and *bateaux feux* of the 'Bulletins Hydrographiques,' published by the Conseil Permanent International pour l'Exploration de la Mer<sup>2</sup>, have been selected from a number which have been maintained more or less regularly by the member nations of the Council since the last war. As a whole they provide a mass of information on salinities and temperatures *at the surface* by means of routine methods at positions along specified routes. As Lumby (1935) has pointed out, they provide the only standards whereby changes from year to year can adequately be assessed, and it is unfortunate that some of them should have been discontinued in later years, and others reduced from weekly or monthly to quarterly or less regular sampling. Apart from the relative uniformity of the methods, their value lies in their spatial and temporal standardization, and it is remarkable that, as far as one can see, so little use should hitherto have been made of them. The positions of those we have selected appear in Text-fig. 1.

We should like to express our thanks to Dr. J. N. Carruthers, Commander J. R. Lumby and Dr. L. H. N. Cooper, who have kindly read and commented on this paper whilst in proof.

<sup>1</sup> The possible introduction of other continuous methods for recording physical data has been under consideration in this department.

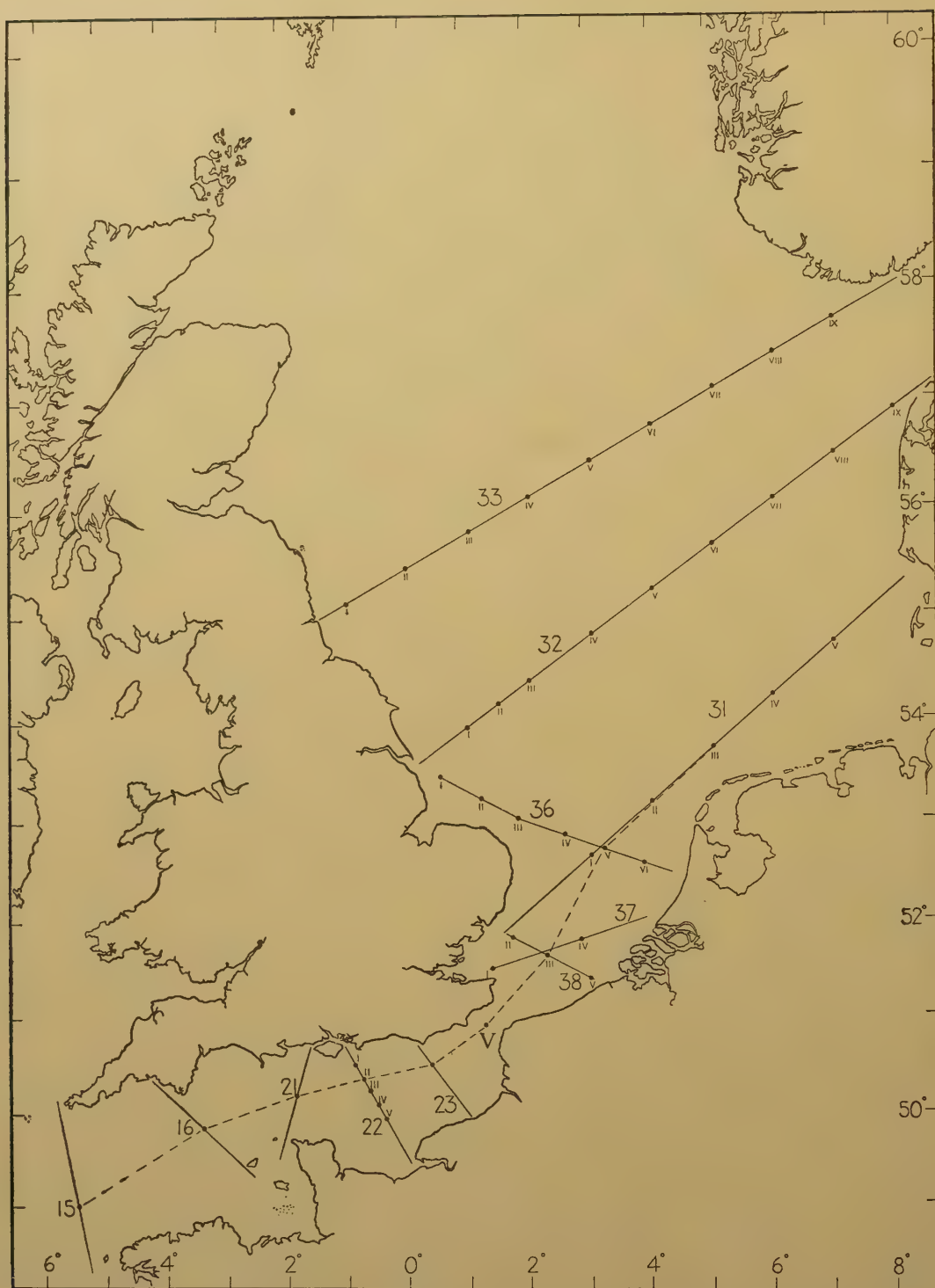
<sup>2</sup> We must express here our gratitude to the Conseil Permanent for their kindness in supplying these data regularly in a form more convenient to us than that provided by the Bulletins.



## SIGNIFICANCE OF THE DATA.

In this review the greater use will be made of salinity data, although temperature data will be used for some purposes. The methods whereby such data have been obtained were discussed by Lumby (1935). Whilst they have some defects, the evidence suggests that in the shallower waters of the North Sea and the English Channel, such surface estimates of salinity are reasonably representative of conditions in the whole water column, and more certainly of the upper part of it. In addition to providing extensive evidence of the general conditions, they should, therefore, be of value in relation to the distribution of plankton at ten metres depth. Surface estimations of temperature are more likely to deviate from those beneath them, but the evidence of trends shown by large numbers of records may be useful. For the more northerly water (*e.g.* Route 33), however, it is necessary to consider further whether the surface data are adequate to the purpose, and it is useful to have some general measure of the probable maximal deviations of surface data from, say, those of water at ten metres depth.

One measure of such differences is provided by the samples taken by Graham and Harding (1938) on a line through the English Channel, into the Southern Bight and through the "Gateway" between the Dogger Bank and the English coast in 1935-37 (their figs. 2-4). The isolines are nearly vertical through the Channel and up to the Humber region, and even in the "Gateway" region there were no great differences (*i.e.* from the biological point of view) within the superficial waters. Further evidence is provided by Graham (1938, figs. 5-12) along lines through the "Gateway" as far north as  $55^{\circ}$  N. in 1934-35. Although at times there were signs of stratification in the north-west, very rarely do the differences between the salinities at the surface and at ten metres exceed  $0.1^{\circ}/_{\infty}$ , or the temperature differences exceed  $2^{\circ}$  C. To take further examples, Savage and Wimpenny (1936, figs. 25 and 26) give data for sections across the "Gateway" in 1932-35, and again there are few important differences in the upper layers. The proportion of salinity differences exceeding  $0.1^{\circ}/_{\infty}$  is under 5%, whilst seldom is a difference of as much as  $1^{\circ}$  C. recorded. Considerable temperature differences existed between the surface and bottom at times, although salinity differences were normally slight, and may have been expected to be even smaller over the shallow waters of the Dogger. Immediately to the north, and particularly to the east of the Dogger, where the water is deeper again, there is possibility of greater differences, although there is no extensive data for this region. As a measure of differences which may exist under such conditions, and probably more extreme, we have examined the abundant data more to the north of our area. These show that usually there were only large differences of salinity when the surface waters were very brackish, and that even these differences were seldom of an order such as to lead to any confusion regarding the nature of conditions at ten metres as deduced from surface samples. More precision is given by



TEXT-FIG. 1.—Showing the positions (•) of the stations on the international routes for which data have been abstracted from the 'Bulletins Hydrographiques.' The arabic numerals, 15, 22, 32, etc., are those used in the 'Bulletins' to signify the different routes, whilst the station numerals, I, II, III, etc., correspond with those used in Text-figs. 2-9. The Varne Light-vessel is denoted by the letter V. Those stations connected by a broken line have been selected to form the *ad hoc* route of Text-fig. 13.



consideration of the whole of the data for 1934 and 1937<sup>1</sup> at these two depths in the North Sea north of  $54^{\circ}$  N., and exceeding  $24.99^{\circ}/_{\infty}$  at the surface ('Bulletins Hydrographiques' for 1934 and 1937). Results show that when the surface waters exceeded  $34.5^{\circ}/_{\infty}$ , only in 35 samples out of 502 was there a greater difference than  $0.1^{\circ}/_{\infty}$  from the waters at ten metres (and in only 8 was it greater than  $0.2^{\circ}/_{\infty}$ ). With lower surface salinities there were greater differences, but even with salinities between  $25^{\circ}/_{\infty}$  and  $27.49^{\circ}/_{\infty}$  the average difference was not much more than  $1^{\circ}/_{\infty}$ . It is probable that the layering of the water does not seriously affect any deductions regarding the environment of the plankton at ten metres, because stratification is normally below that depth. Such a conclusion has a wide importance for the Recorder surveys since, in the extended area of 1938-39, the records were regularly taken over much deeper water than before, and it is necessary to know how far surface hydrological information may be relevant under such conditions. There is reason to believe that it will be adequate for many purposes.

#### METHODS, ETC.

The routes and stations from which hydrological data have been selected are shown in Text-fig. 1. They may be compared with the charts shown in the 'Bulletins Hydrographiques' since 1932, the same numbers being used here to denote the regular steamship observations. For simplicity the various stations on these steamship routes have been denoted by Roman numerals, both in this figure and in the figures showing graphs of the data (I denoting the stations on the English side). A number of these, *e.g.* on route 32, have apparently been made regularly in the same places (*i.e.* the longitude and the latitude for each station are given as identical on each occasion). On others, *e.g.* Route 36, these vary from time to time, whilst not always have the same number of stations been sampled. For these reasons those stations have been selected which have been sampled most often, *i.e.* truly routine ones. Their average positions have been found, and for practical purposes these have been used as if constant; random samples of the errors involved in this assumption show that rarely do they exceed five miles in any direction. Other differences from the data in the 'Bulletins Hydrographiques' concern the omission of certain stations which did not seem particularly useful for the present purpose (*e.g.* a coastal station in Route 36), whilst in one case selected stations from two routes have been combined and used as if on one route for economy and simplicity (Routes 37 and 38). For all these stations the data have been abstracted from the Bulletins as provided and used without any attempt at correction. There are good reasons for believing that some errors are present in the original data (*e.g.* the unusually low salinities in December, 1935, on Text-fig. 5), but we have decided (see also Lumby, 1935)

<sup>1</sup> The choice of these two years was made at random in order to provide evidence on this point. Temperature differences were also slight on the whole; for all 1937 surface values between  $3^{\circ}$  and  $14^{\circ}$  C., in only 12 cases out of 375 did the difference exceed  $1^{\circ}$  C.

that it is better to include even these unlikely data, since corrections and omissions may well lead to greater confusion and error than the original mistakes.

In order to lead up to the period of the plankton survey, we have made use of data from January, 1930, wherever possible. The following details regarding the individual routes are relevant:

Route 33. Shields-Oslo. (Text-figs. 2 and 3.) Usually weekly samples on the meridians of longitude from  $1^{\circ}$  W. to  $7^{\circ}$  E. This route is to the north of the plankton data.

Route 32. Hull-Copenhagen. (Text-figs. 4 and 5.) Usually weekly samples on the meridians of longitude from  $1^{\circ}$  E. to  $8^{\circ}$  E., with an additional station at  $1^{\circ} 30'$  E. This route corresponds exactly with the Copenhagen line of the plankton records, the data being obtained by the same ship.

Route 31. Esbjerg-Harwich. (Text-fig. 6.) Selected sets of weekly samples on the meridians of longitude from  $3^{\circ}$  E. to  $7^{\circ}$  E. (from June, 1930, only). Whilst this route corresponds to the Esbjerg plankton line (in use from 1936), the data were often obtained from different ships on different days.

Route 36. Hull-Amsterdam. (Text-fig. 7.) Samples<sup>1</sup> grouped around the 5th, 15th and 25th of each month at six selected stations (for mean positions, see Text-fig. 1). There are no data for 1930 and part of 1931. Although taken at different times and by different ships, the Western part of this route lies fairly close to the corresponding part of the Rotterdam plankton line. The Eastern part of the route deviates well to the north of the plankton recorder line.

Routes 37 and 38. Gravesend-Hook of Holland and Harwich-Flushing. (Text-fig. 8.) Two stations from the first route have been combined with three of the second. The samples<sup>1</sup> were collected in a manner similar to that for Route 36, and the data have been graphed as if they were one route for convenience and economy, their mean positions being shown in Text-fig. 1.

Route 22. Southampton-Le Havre. (Text-fig. 9.) Approximately weekly samples in sets of five or four stations (usually alternate, omitting the most continental one) and approximately at intervals of  $9'$  longitude.

Varne Light-vessel (V, Text-fig. 1.) Average monthly values from samples taken some eight times each month. These, and Routes 22, 37 and 38 lie to the south and west of our plankton data.

In addition to the data mentioned above, which have been used and plotted more fully, others have been abstracted on similar principles for incidental reference. These are Routes 23 (Newhaven-Dieppe), 21 (Southampton-St. Malo), 16 (Plymouth-Guernsey), 15 and 10 (variously crossing the mouth of the English Channel along similar courses), together with the Sevenstones Light-vessel. Reference is also made to certain individual stations for special purposes.

A suitable graphical method was not at once apparent for the illustration of

<sup>1</sup> Unlike those for the other routes, the values given for these observations on each occasion represent the mean values for a number of observations made during five days prior to and five days following the "mean" date,



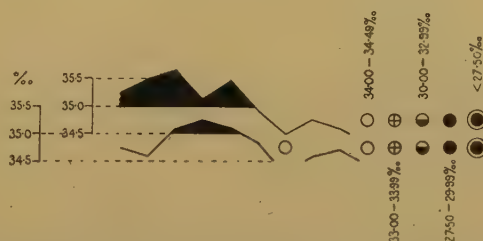
the major data. The widely varying salinity ranges make unsuitable any simple method of graphing, since a linear scale which clearly shows the total variations in salinity tends to minimize the important, but much smaller, variations within the higher ranges. Since we wish to show in one figure as many data as possible, both for comparative purposes and for economy, a simple graphical method, with a linear scale, is used for salinities above  $34.49\text{‰}$  (the values over  $34.99\text{‰}$  being shown in black), whilst below this value a range of symbols is used to show the different types of more or less brackish water (see scale below for Text-figs. 2-9). In this way one can distinguish at a glance the regions of most saline water (blackened-in) from those of moderate but still appreciable salinity (line), and both of these from the remaining regions, of quite different constitution, in which the varying brackishness of the water is shown by the increasing density of the circular symbols.

Reference to Text-fig. 1 shows that not all the mean positions of the stations (*e.g.* on Route 36) are equally spaced, and even where constant positions have been given (*e.g.* Route 33) it is uncertain that the true positions were in fact so regular. In view of the small variations involved, it has been thought more convenient to present the data as if all the stations on any one route had been equidistant, and so constant in position. Thus the successive sets of data for any route can readily be compared when arranged as vertical series, in time order for each year, the years appearing in consecutive columns. The method is similar to that adopted for the continuous plankton records in earlier bulletins. All data for one station in any year may be found in a vertical line under the appropriate Roman numeral, whilst lines of stations at similar times of the year may be found in horizontal line, the letters J, F, M, etc., representing the months.

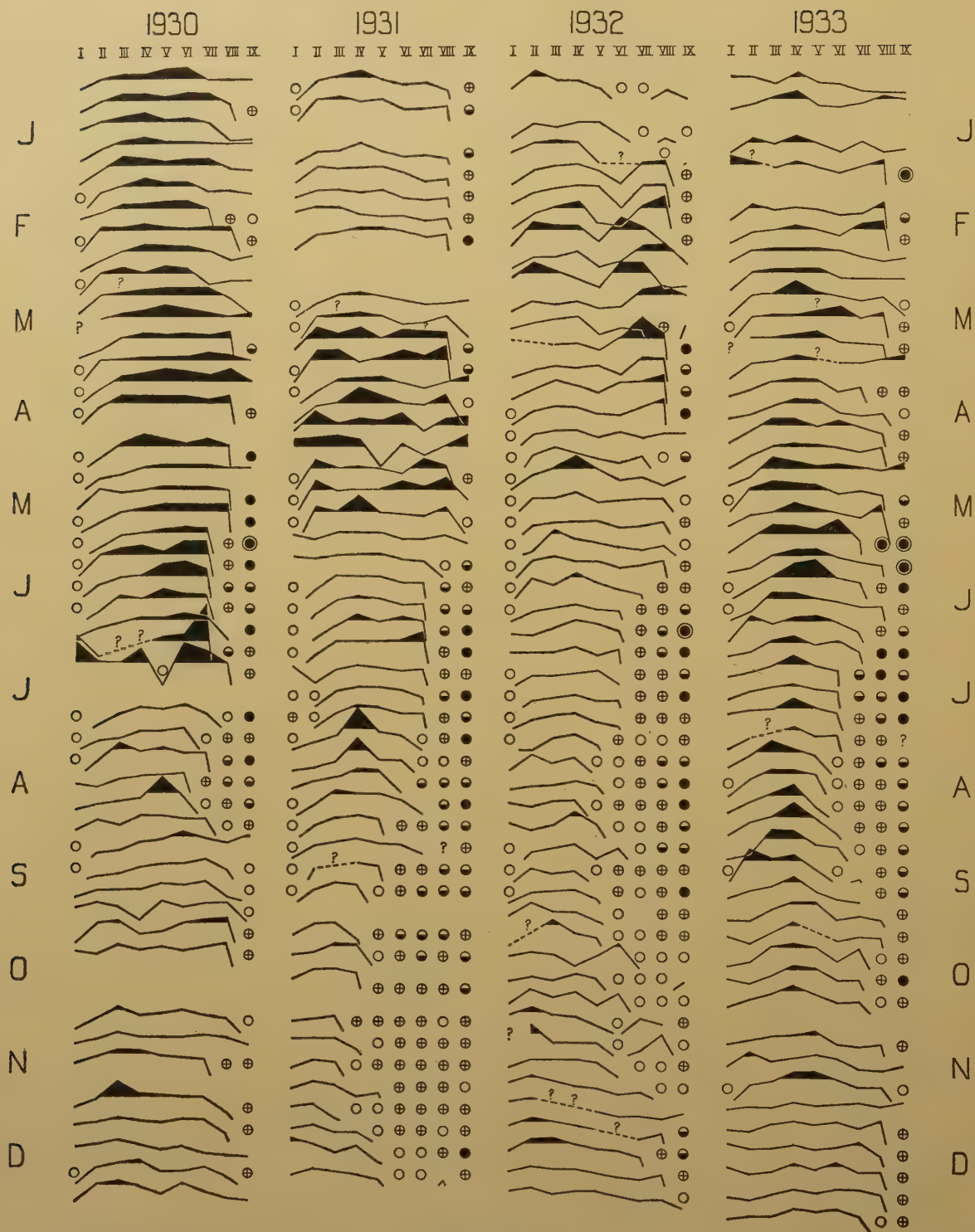
Few other symbols have been used in these graphs, but reference should be made to certain conventions. Where observations denoted by linear methods and those shown by circular symbols are adjacent, the trend between them is denoted by a line from the last "graphical" value, tending towards the position the other would have had had it been shown on the "graphical" scale, but stopping short on the  $34.5\text{‰}$  baseline. The rate of change of salinity is thereby shown. Similarly, within the usually broad area of lower salinity values, such higher ones as appear are shown "graphically" in a similar manner. In the extreme cases these may appear on the  $34.5\text{‰}$  line as points only.

Where odd observations have failed, the omissions have been denoted by the symbol "?" and, if in the graphical sections, the adjacent stations have been connected, where possible, by broken lines.

Three sets of abstracted data have been obtained. For the first, Text-fig. 10, it has been useful to provide a numerical measure of the annual changes on the



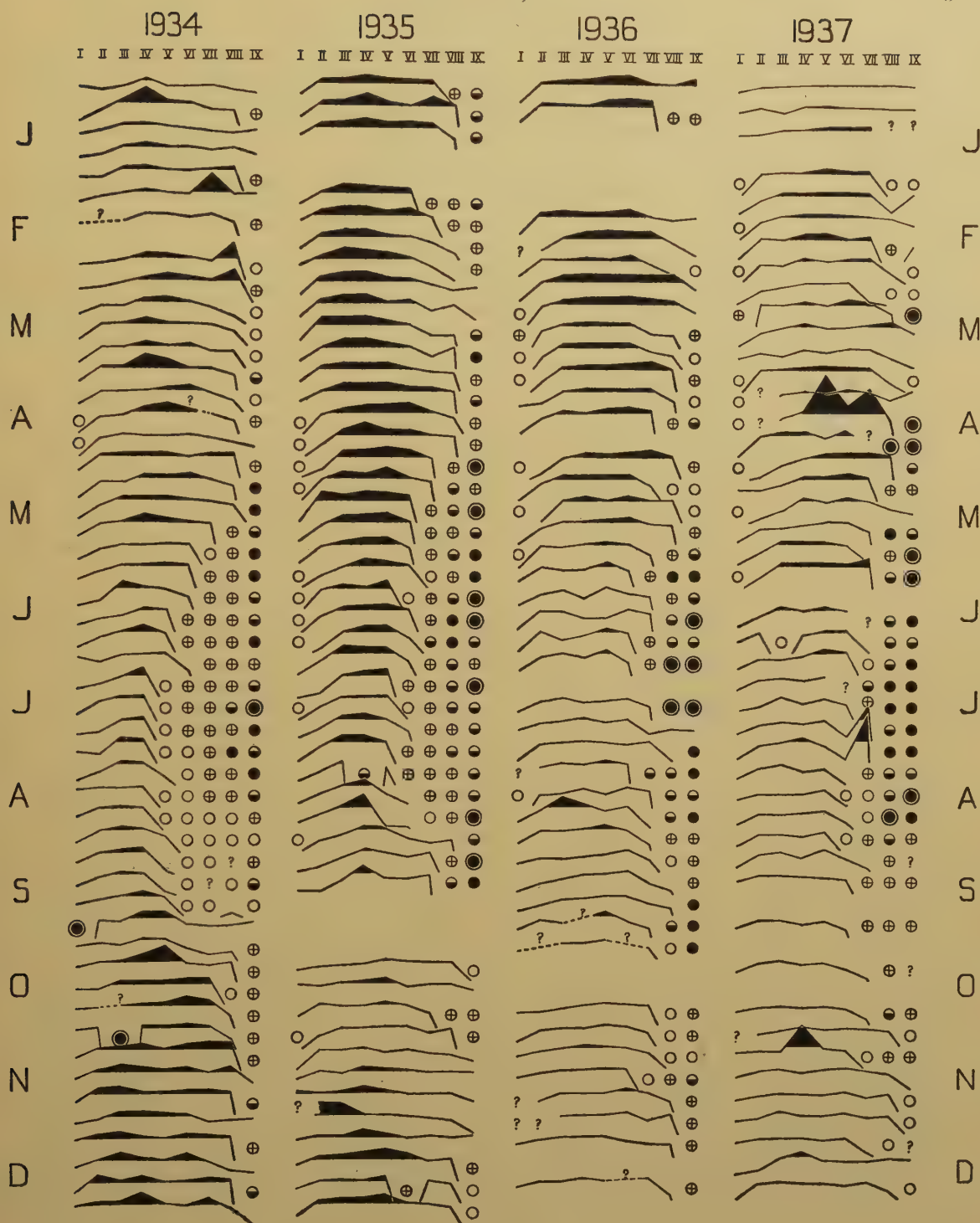
TEXT-FIG. 2a.—Scale of salinities for Text-figs. 2-9 and 13,



TEXT-FIG. 2.

TEXT-FIGS. 2 and 3.—Route 33 (Shields-Oslo). Showing the surface salinities at stations I-IX (Station I being that nearest to the English coast) at weekly intervals during 1930-37. For each weekly set, the linear graphs show the varying salinities above 34.49‰, the blacked-in portions being above 34.99‰; the increasing brackishness of waters below 34.49‰ is denoted





TEXT-FIG. 3.

by the increasing density of circular symbols (see scale in Text-fig. 2a on p. 7, and also text). The sets of graphs are arranged in eight vertical series, one for each year; the months, within which the weekly graphs fall, are denoted by the letters J, F, M, etc., down the sides of the vertical series, each letter indicating the middle of the corresponding month.

different routes, and we have plotted for certain of them, against time, the number of occasions in each month when salinities exceeding certain values were recorded so that, for example, one can compare the abundance of water exceeding  $34.99^{\circ}/_{\infty}$  salinity in different seasons and years.<sup>1</sup> From these we have been able to derive (Text-fig. 12) a general impression of the trends on the different routes by the method of "moving averages"; whilst such impressions can only be most approximate, they may be as useful as can be expected from the data. For the second type of abstracted data (Text-fig. 13) we have selected certain stations from the standard routes to form a sequence representing a "route" extending from the mouth of the English Channel, through the Straits of Dover, into the North Sea (broken line in Text-fig. 1); the mean monthly salinities along this "route" are shown at monthly intervals by methods similar to those adopted in Text-figs. 2-9. In the third abstraction the data for most of these stations are shown by linear graphs in time sequence, so that the times of occurrence of particular types of water at certain positions may be readily compared (Text-fig. 14).

With these matters in mind the routine data may be reviewed, first for the North Sea stations, and then for the Channel waters.

#### THE BASIC HYDROLOGICAL DATA.

Route 33 (Text-figs. 2 and 3) shows two chief types of surface water. The western water was mainly of higher salinity, whilst the eastern water usually provided lower values, although sections of brackish water appeared in the extreme west, just as higher salinities were at times found in the east. The symbols for the lower salinity water present a useful picture of the varying expansion of the brackish surface water off the mouth of the Baltic. Whilst there was usually a maximum spread of brackish water in the late summer months, it varied greatly from year to year. In 1930 it was only moderate in extent and was greatly exceeded in 1931, when the maximal area was recorded in the autumn. It then occurred progressively earlier up to 1935, varying in extent but generally decreasing after 1934, whilst in 1936 and 1937 it was, on the whole, rather later. In distinction from the spread of water below  $34.5^{\circ}/_{\infty}$ , the number of stations giving samples below  $30^{\circ}/_{\infty}$  was much greater during the second half of the period (and particularly 1937) than in the first half; on the other hand, the salinities in this region were quite high at times. In association with the variation of the Baltic water, the extent of the higher salinity surface water varied, this being particularly small in the autumn of 1931 and the summers of 1932 and 1934, although in the latter year the actual salinities were quite high. On the whole the higher salinities appeared in the spring and summer, and reappeared in the autumn. After persisting for a long period in 1930, the salinities over  $35^{\circ}/_{\infty}$  were much scarcer in 1931

<sup>1</sup> This has certain disadvantages when compared with mean salinities, but it avoids the difficulties introduced when the means of values taken in very different types of water may be quite unrepresentative of any conditions recorded.



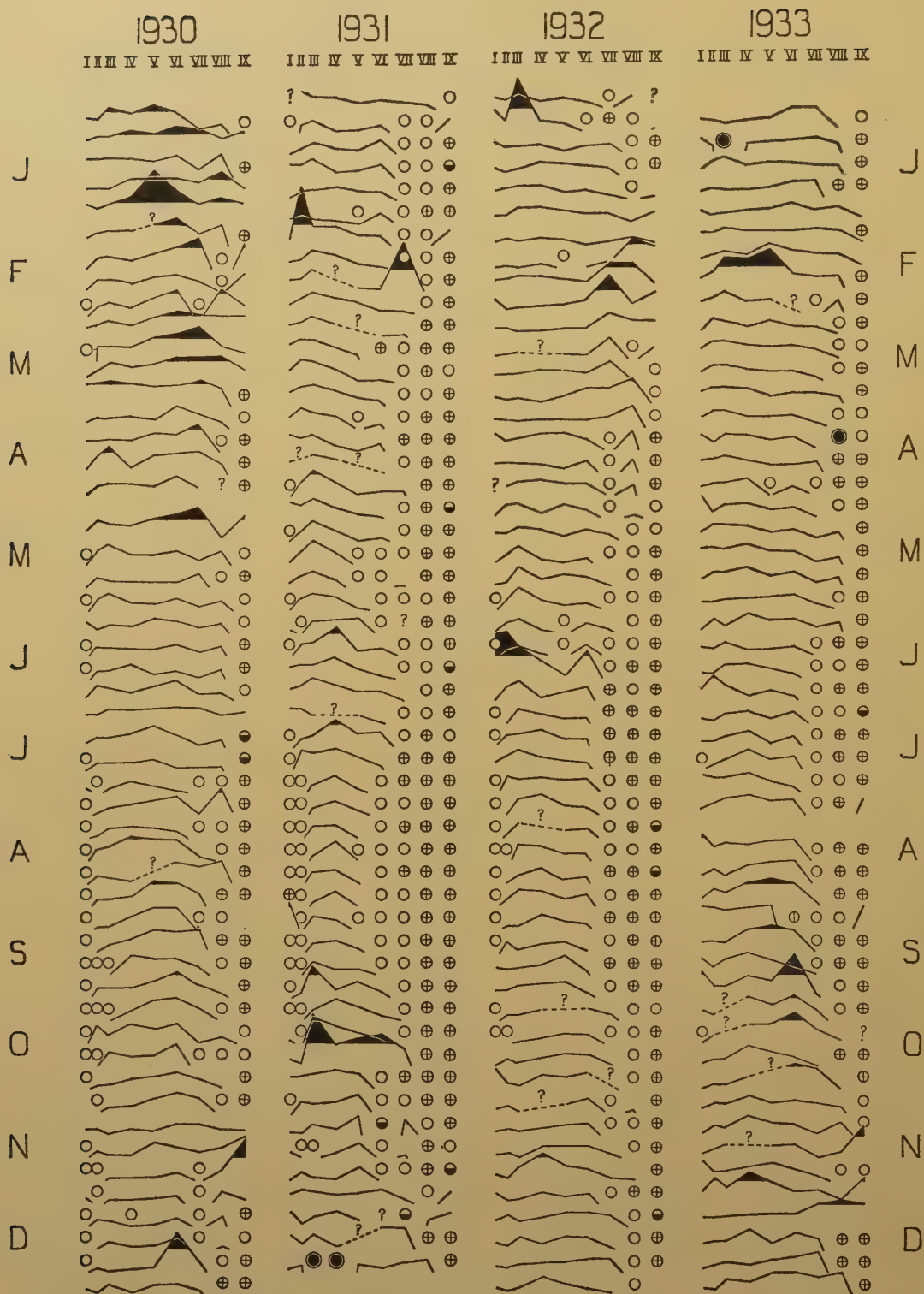
and 1932 and then steadily increased, to attain a period of consistently high values from the autumn of 1934 until the summer of 1935. They then decreased again, until in 1937 they were nearly as low as in 1932. Other points concern the spatial and temporal relationships of the different water masses (*e.g.* the shifting zones of salinity exceeding  $34.99^{\circ}/_{\infty}$ ), the persistence of particular formations (*e.g.* in the summer of 1934) and the sudden changes in time and space. In particular, the extent of the low salinity water at the western end of the line decreased from 1931 to 1934 and then increased again; whilst it is probable that individual surface samples of low salinity are likely to be unreliable indications of the conditions in the water column, yet broad annual changes such as appear here may have significance for the plankton production, and are in themselves signs of important events in the sea.

Turning now to Route 32 (Text-figs. 4 and 5) we should emphasize that on this line the water samples were taken by the same ship and, when the plankton recorder was used, at the same time as the plankton samples.<sup>1</sup>

The salinities were generally lower than on Route 33, but rather similarly distributed. The eastern area of low salinity was most extensive in 1931 and appeared to persist longer than on Route 33, whilst it tended to vary less and was less brackish, presumably since it does not include waters flowing from the Baltic. The areas of high salinity in the west were less saline than on Route 33, and they were least marked in 1931, increasing to 1935, and then decreasing again. On the whole they were more equably widespread on this route, but there were periods of distinctly high salinities over to the east in the winter and spring. The area of low salinity water in the west was more marked and occurred rather later than on Route 33; it was most evident at the beginning and end of the eight-year period. In general there was not the persistence of isolated patches of high salinity surface water such as occurred on the northern route, but a striking feature was the occurrence of patches of high salinity water with no obvious precedents on Route 33, in contrast with the other occurrences of such water, either following or associated with similar water on 33. Such patches were generally found in the autumn and winter, but also occurred in the summers of 1936–38.

Route 31 (Text-fig. 6) coincides with the Esbjerg plankton line which was started in 1936; although the water samples were not always taken on the same ships, they were often taken on the same dates. Salinities below  $34.5^{\circ}/_{\infty}$  were much commoner here, although high salinities occurred in the autumns and winter records of 1934–35 and 1935–36. The lower salinities were mainly but variably restricted to the north-eastern end of the route, and it seems as if the higher salinity water was spreading northwards on certain occasions; at other times there appear to be pulses of only moderately saline water. The more saline water does not always include the first (*i.e.* the most southerly) station, but usually it does. For

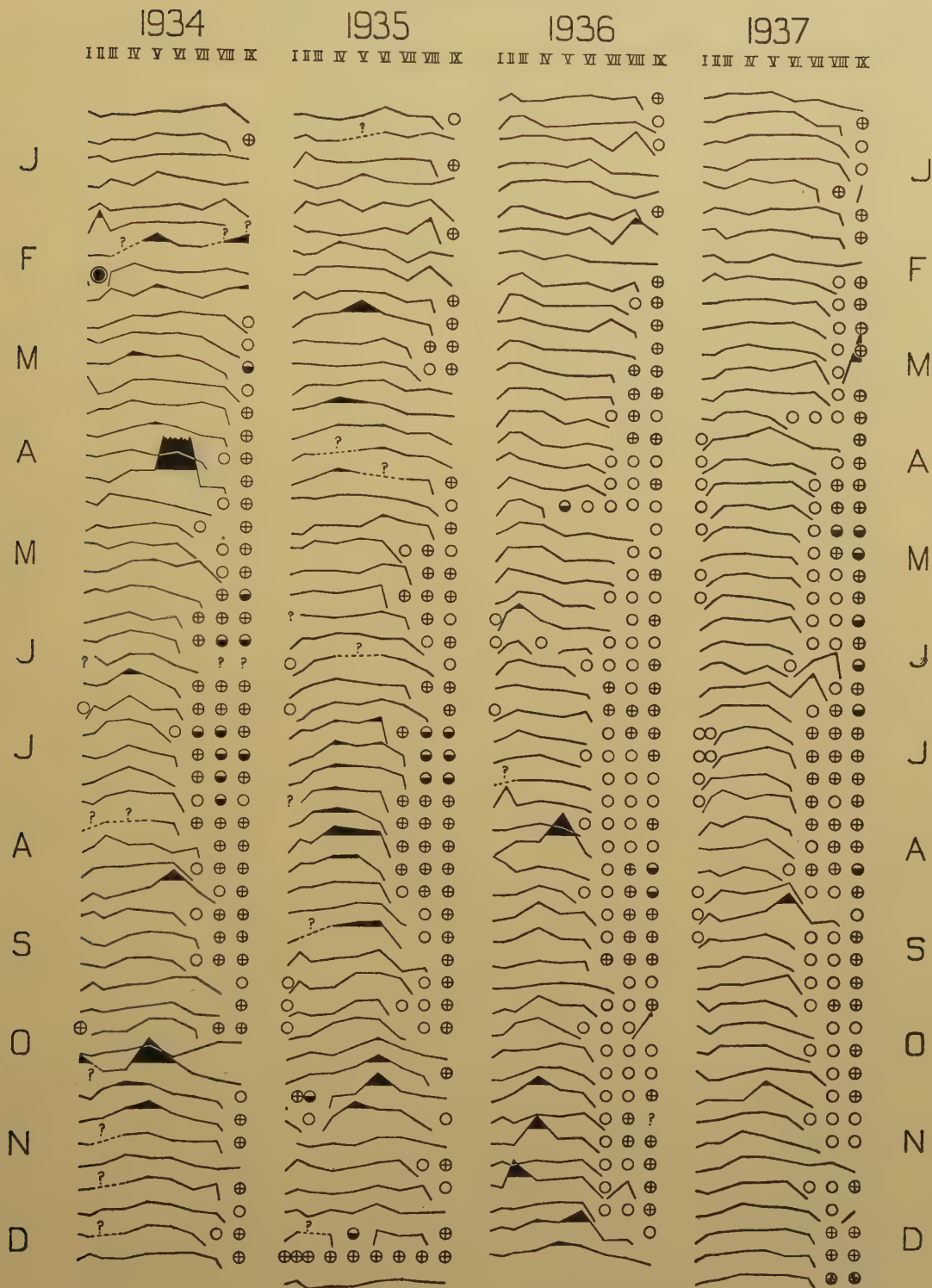
<sup>1</sup> The temperature distributions along this route show that 1933 was undoubtedly the warmest year in this area, with 1934 and 1935 probably following, although there were great seasonal and spatial variations. In particular there were very sharp changes in the spatial relations between the warmer and colder water. The data will be used mainly in connection with plankton observations (Part II).



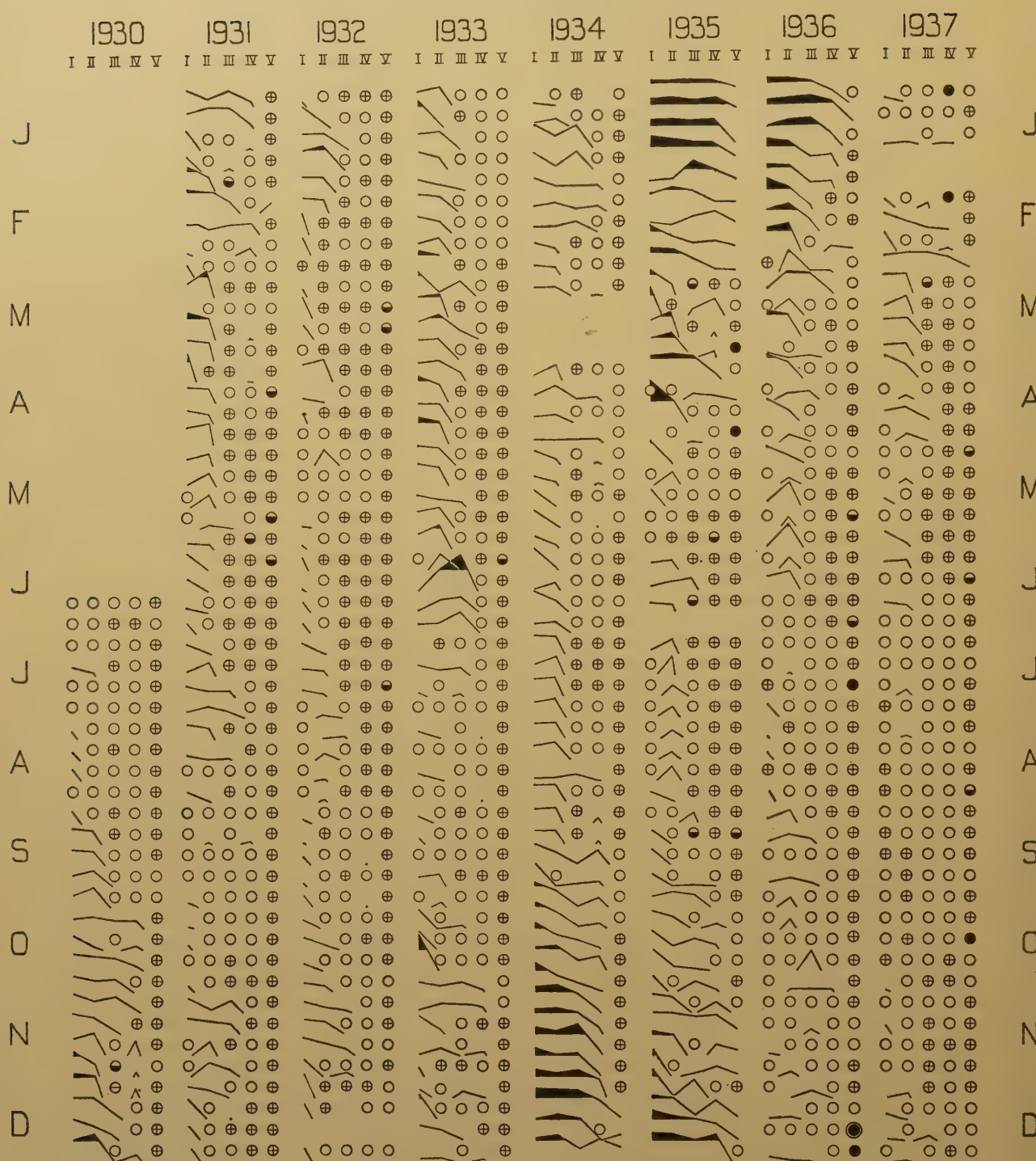
TEXT-FIG. 4.

TEXT-FIGS. 4 and 5.—Route 32 (Hull-Copenhagen). Showing the surface salinities at Stations I-IX (Station I being that nearest to the English coast) at weekly intervals during 1930-37. Details as in legend for Text-figs. 2 and 3.





TEXT-FIG. 5 (see opposite).



TEXT-FIG. 6.—Route 31 (Harwich-Esbjerg). Showing the surface salinities at Stations I-V (Station I being that nearest to the English coast) at weekly intervals during 1930-37. Details as in legend for Text-figs. 2 and 3.



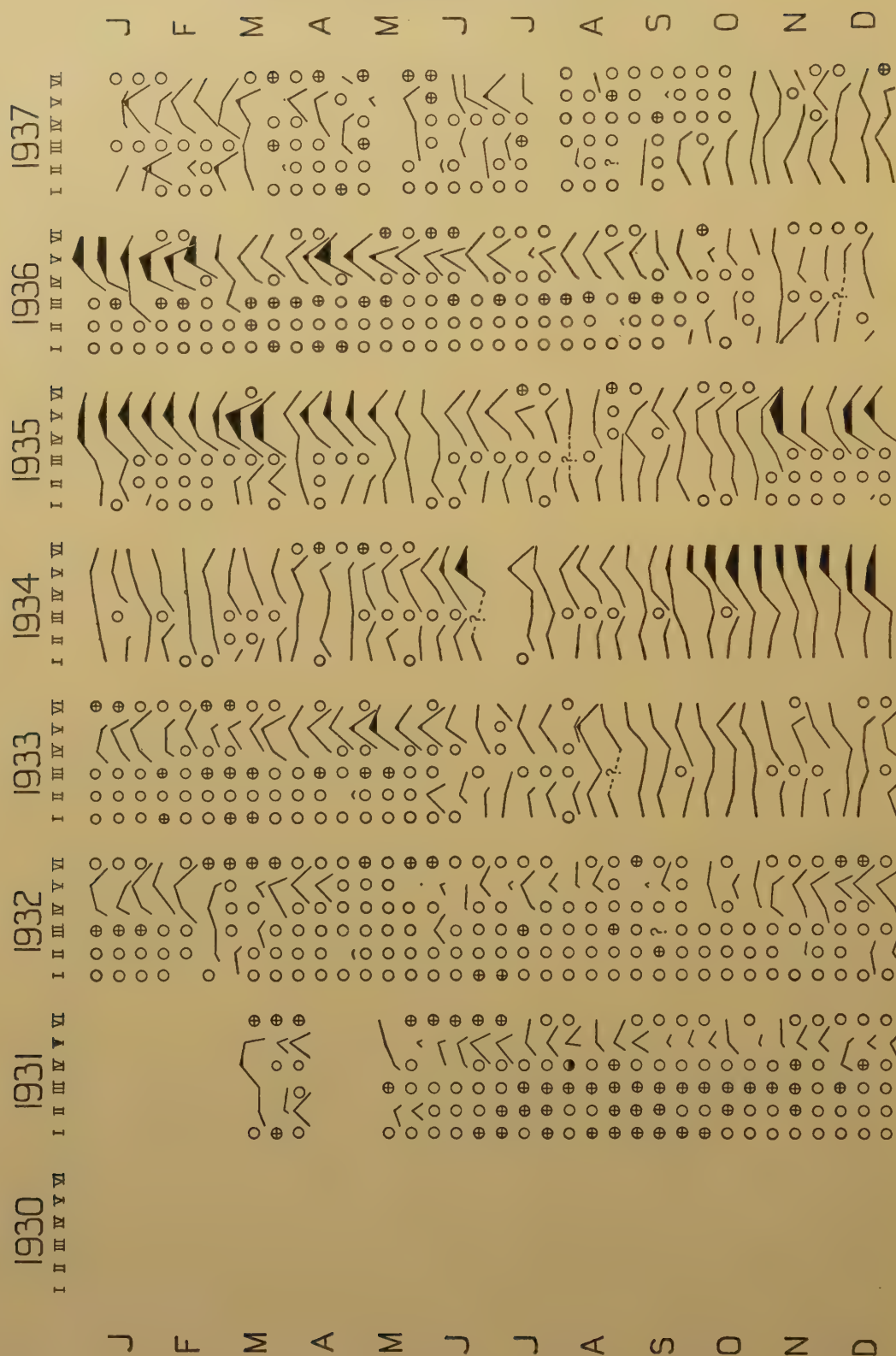
later reference should be noted the long period in 1937, when less saline water covered the whole route, sometimes with quite low salinities in the south.

Whilst there are obvious relationships between Routes 33 and 32, there appear to be no immediate ones between these and either Route 31 or 36, except in the general trend which will be mentioned later. In fact, Route 31, and to some extent Route 36, provide, by their generally lower salinity, a boundary between the more saline surface waters to the north and the south. The western three stations of Route 36 (Text-fig. 7) are close to the standard Rotterdam plankton line, but the eastern ones diverge to the north of it since the route proceeds to Amsterdam. Some of the earlier data are not available. The salinities on the whole were higher than on Route 31, but low salinities were widespread in 1931 and 1932, after which moderate values and then higher ones became general, only to return towards the earlier conditions after the beginning of 1936. Usually the highest salinities occurred on station V, although VI gave at times even higher values. In contrast the western stations were usually more brackish, but the period from July, 1933, to the end of 1934 (together with parts of 1935, 1936 and the end of 1937), when more saline water occurred there, is noteworthy. The whole distribution of the data suggests, as we might expect, that normally there was a narrow channel of more saline water on this route, which extended at times, but which sometimes, as in 1937, disappeared. Station III, perhaps because of its proximity to the coast, was usually of particularly low salinity.

The distribution was generally similar on the combined Routes 37 and 38 (Text-fig. 8), except that the salinities were higher, the channel of higher salinity water was rather wider, and was more towards the west. Usually the samples from station II, but sometimes IV,<sup>1</sup> were the most saline. A complete series of data is available and, as in previous routes, the general salinity decreased after 1930, increased in 1933, and became even higher in 1934, after which it decreased once more. Salinities were particularly high in the late summer, autumn and early winters, whilst there were periods of generally low salinity, as in October, 1931, and June and July, 1937. The most easterly station was below  $34.00^{\circ}/_{\infty}$  without exception, but the western station, inside the Foreland, showed quite striking changes; only in 1934 was it very saline, and then nearly as much so as the central ones.

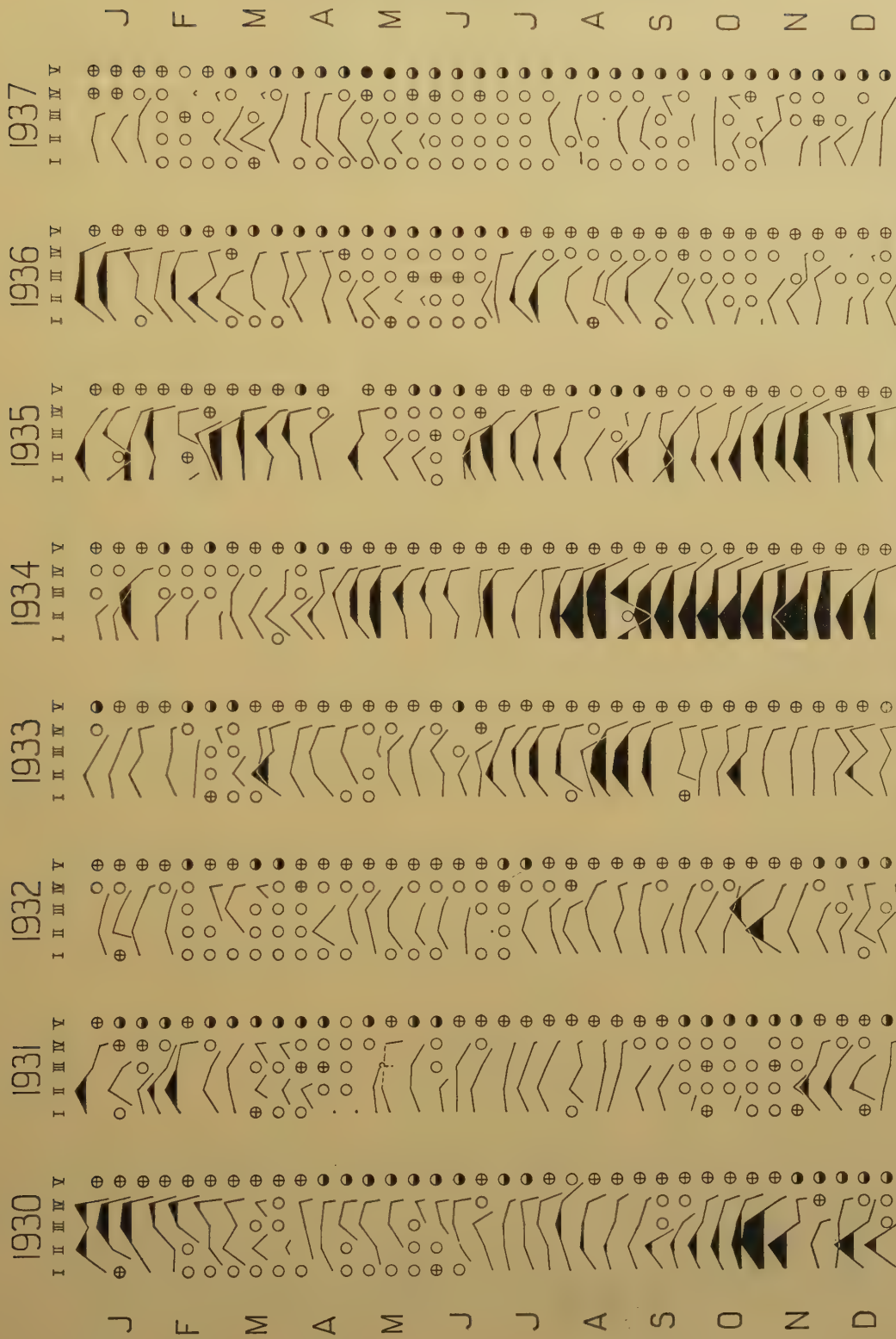
Each of these routes shows more or less marked seasonal reductions in salinity, the individual features of which will be discussed more fully later in relation to the plankton, but taken together they show a striking agreement. After a period in 1930 when salinities were fairly high, they were lower in 1931-32, only to increase again up to 1934 and/or 1935; they were regularly lower in 1936 and 1937, when in some instances unusually low values were recorded. This trend is summarized in Text-fig. 10, where the data for the extent of the higher salinity water (*i.e.* the numbers of occurrences exceeding a given value in each month) are shown graphi-

<sup>1</sup> It is interesting that III rarely provided the highest salinities, although it was nearer the mouth of the Channel and (one might expect) nearly in line with IV along the flow route (Text-fig. 1).



TEXT-FIG. 7.—Route 36 (Hull-Amsterdam). Showing the surface salinities at Stations I-VI (Station I being that nearest to the English coast) at intervals of ten days during 1930-37. Details as in legend for Text-figs. 2 and 3.





TEXT-FIG. 8.—Routes 37/38. (Gravesend-Hook of Holland and Harwich-Flushing.) Showing the surface salinities at Stations I-V (Station I being that nearest the English coast) at intervals of ten days during 1930-37. Details as in legend for Text-figs. 2 and 3.

cally. Although the times of the maxima vary a little—from the autumn of 1934 in the south to the spring of 1935 in the north—the whole series presents essentially the same cycle. Such an agreement is striking, and it is strengthened when we note, in the same figure, that the mean salinity (as well as the numbers of high salinity occurrences) at the Varne Light-vessel showed a similar trend.

In relation to the facts just reviewed, it will be remembered that Tait (1935) reported increasing salinities in the north-western North Sea during the period 1930–34, whilst in later years (‘ Reports of the Fishery Board for Scotland ’) these were said to have been decreasing. The observations were associated by Tait with the effects of a cycle of Atlantic influence in that area, and he considered that a maximum was probably attained in 1934 (see also Van Riel, 1936), the influence decreasing during 1935 in association with the increased polar activity which began during the summer of 1934 (Tait, 1936). Eggvin (1937) records a progressive decrease in salinity from 1935–36; whilst by 1937 it is reported that “ the inflow of Atlantic water into the northern North Sea . . . appears to have been weaker than for at least five years ” (‘ Scottish Fishery Board Report for 1937 ’). The report for 1938 suggests this recession to have continued into that year. There thus appears to have been a similar cycle over the whole area extending from the North-western North Sea through to the Straits of Dover.

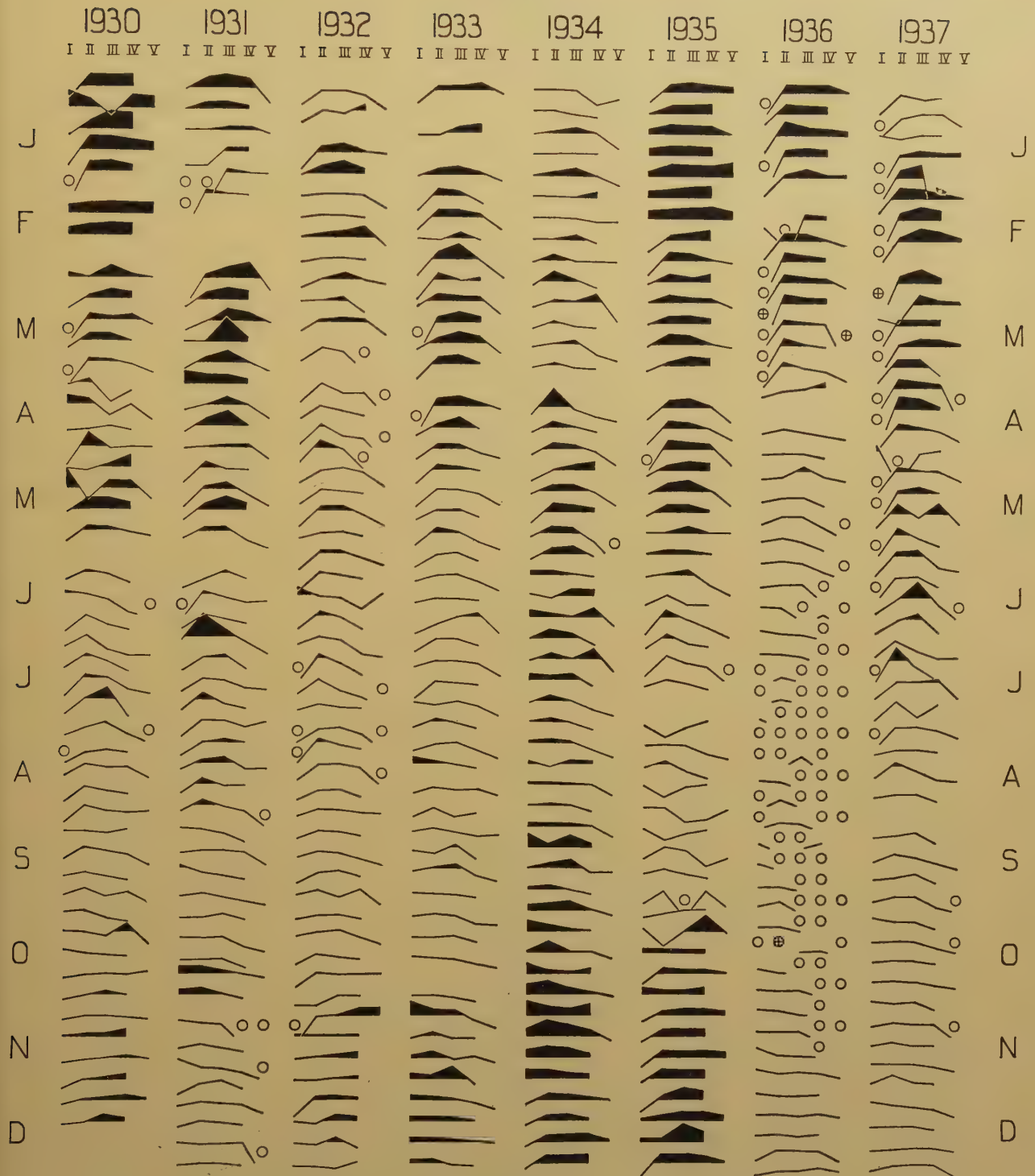
In order to see how far this trend extended we abstracted some of the English Channel data. Those for Route 22 are shown fully in Text-fig. 9. A period of high salinities in the springs of 1930 and 1931 was followed by lower ones in the springs of 1932–34 (rather higher in 1933), and then in the summer of 1934 the salinity began to increase, developing further in the autumn, to give widespread high values in the spring of 1935. It then decreased in the summer, and rose again in the autumn and winter of 1935–36, only to decrease to abnormally low values in the next summer. Although it was again higher than in some years in the spring of 1937, the net effect was of a decrease leading to low values for this route in the autumn. Broadly speaking a similar result is shown by other Channel lines which cannot be shown fully here. Data abstracted from Routes 15 and 22 are shown in Text-fig. 10, along with those for the North Sea. It will be seen that both Route 22 and Route 15 provided very low salinities in 1936.

#### DISCUSSION.

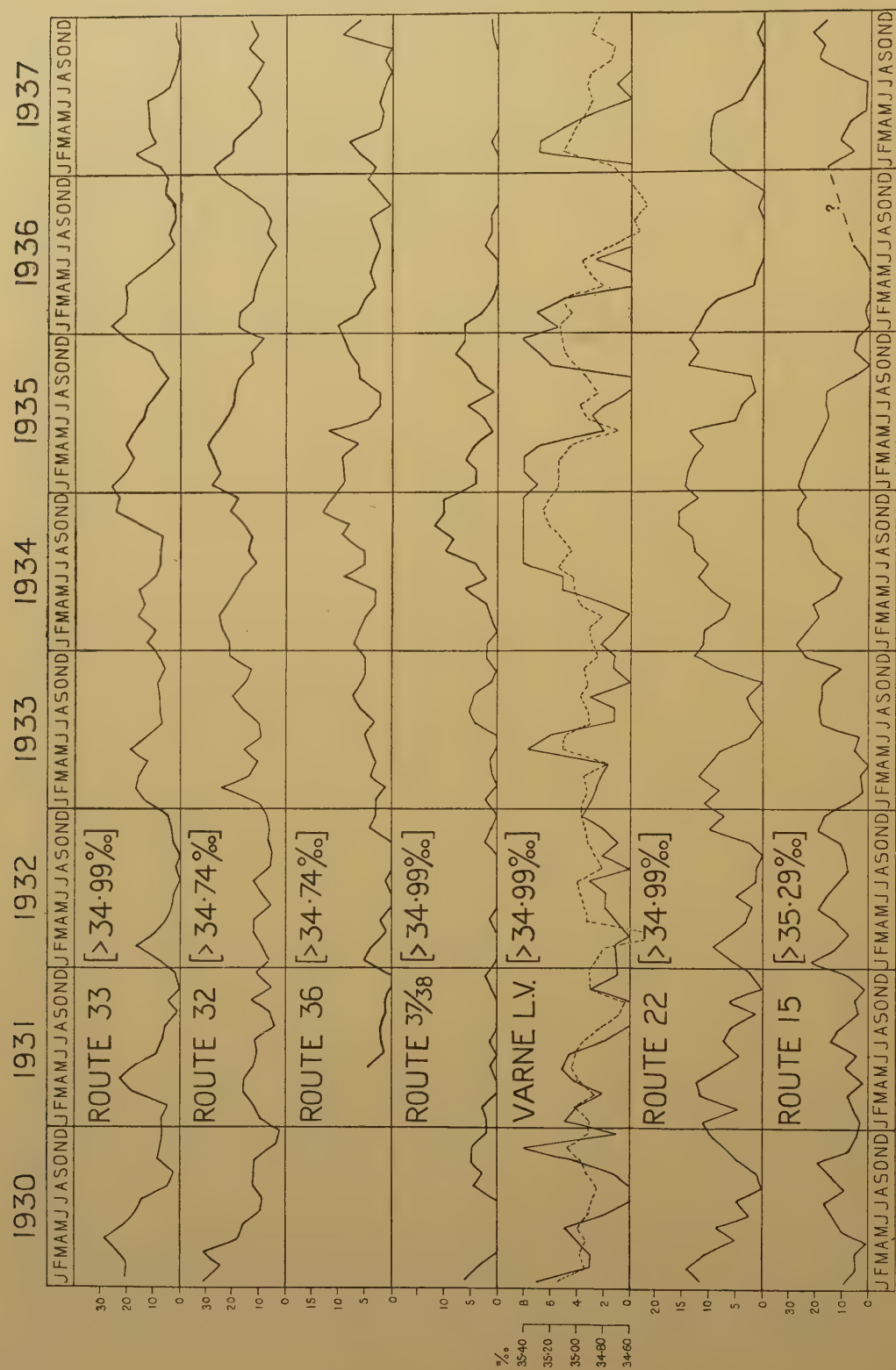
##### *The Salinity Trend during 1930–37.*

It seems necessary to conclude from all these observations that during the period of the plankton survey, 1932–37, there was an increase of salinity up to the period 1934–35, followed by an equally marked decrease, over an area which extended from the Northern North Sea right through the region of our plankton samples down to the southernmost parts of the North Sea and, in varying degrees, to the western end of the English Channel. In order to obtain a better idea of this trend, which is liable to be confused by the local and considerable seasonal



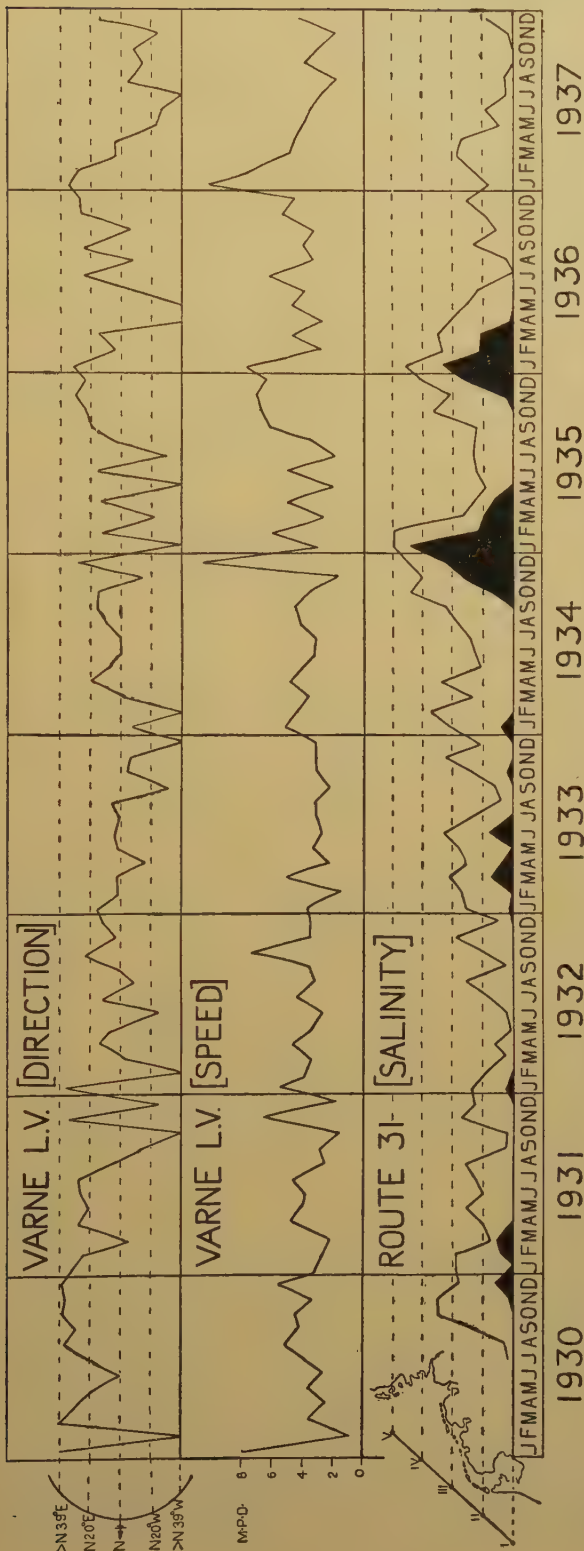


TEXT-FIG. 9.—Route 22 (Southampton-Le Havre). Showing the surface salinities at Stations I-V (Station I being that nearest to the English coast) at weekly intervals during 1930-37. Details as in legend for Text-figs. 2 and 3.



TEXT-FIG. 10.—Showing the frequency of surface salinities exceeding particular values along Routes 33 (exceeding 34.99‰), 32 (ex. 34.74‰), 36 (ex. 34.74‰), 37/38 (ex. 34.99‰), 22 (ex. 34.99‰), 15 (ex. 35.29‰) and the Varne Light-vessel (ex. 34.99‰), month by month during the years 1930-37. For comparison are shown the monthly variations in salinity at Varne (broken line).





TEXT-FIG. 11.—Showing graphically the monthly variations in direction (see inset compass scale) and speed (miles per day) of the Varne current (Carruthers, 1935, and circulated data). For comparison are shown the variations in mean monthly extension between Stations I and V along Route 31 (see Text-fig. 1 and inset chart) of surface salinities exceeding  $34.49\text{‰}$  (line) and  $34.99\text{‰}$  (blackened-in).

variations, the data for representative routes in Text-fig. 10 have been treated by the method of moving averages.<sup>1</sup> The resultant trends are shown in Text-fig. 12, and appear to have culminated variously between October, 1934, near the Straits of Dover and January–February, 1935, in the north and west. Particularly on Route 33 it appears that the high salinities persisted for a longer time in 1935 than the results of Tait (1936) and Van Riel (1936) suggest for the water to the north. There were signs of subsidiary maxima in 1932–33 (most marked on Route 15), and there is a suggestion that, as a whole, the cycle was somewhat earlier in the west than in the north. Although there were slight differences in phase, the similarity in the main period of maximum gives the immediate impression that over the whole area the salinity of the surface water must have increased more or less simultaneously.

Attention elsewhere does not seem to have been drawn as yet to the existence in the Channel of a cycle of salinity resembling that in the North Sea during

<sup>1</sup> This method is described, for example, by Rhodes (1933, p. 214).

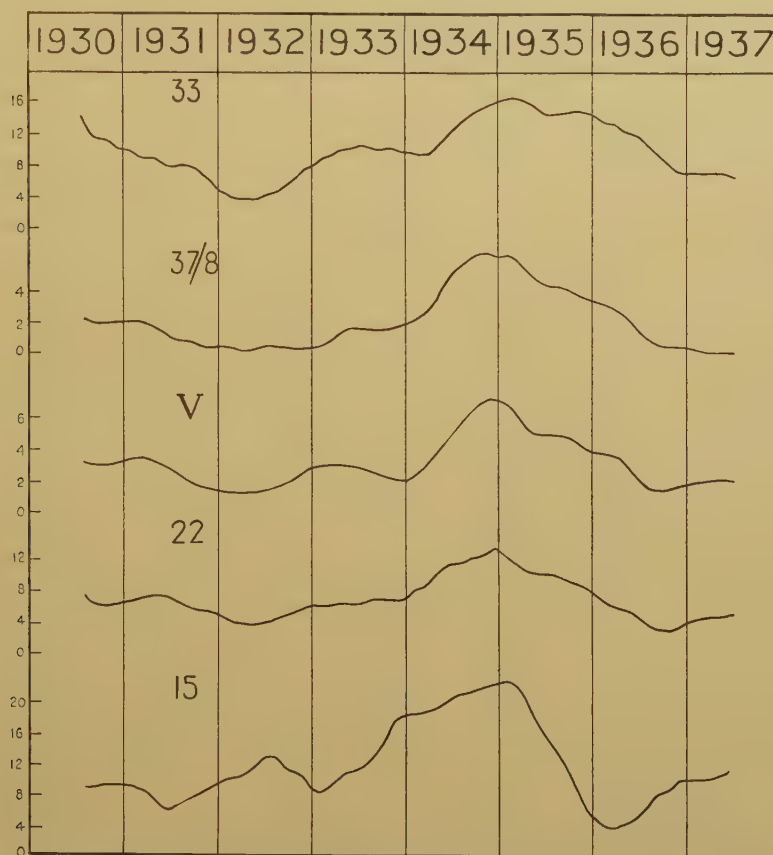
these years, but we must remark here on another Channel phenomenon, *i.e.* the remarkable decrease in the quantities of phosphate available for phytoplankton production. The values off Plymouth have been much lower since 1930 than in earlier years (Cooper, 1938), whilst there have been parallel changes in the abundance of various marine animals (Kemp, 1938, reviewing various data). Within the period of low values it is of interest that the quantities of phosphate decreased rather irregularly until the winter 1934–35, when a minimum was reached, whilst in the three succeeding winters distinctly higher values were recorded, although still well below the means for the years 1922–30. It is, however, important to record that workers in this area were unable to report any clear associations between these changes and the local hydrographical data. “The plain fact is that the observations we have of salinity and temperature do not fit into the picture” (Kemp, 1938; see also Harvey, 1945, although Cooper, 1938, has suggested a connection with the Varne currents). With the exception of the signs of some parallelism in that the winter phosphate maxima became generally poorer as the salinity increased, and then rather less poor, as it decreased, we can add little to this statement, but the indications of the winter 1934–35 being the most “unusual” period may be important.

The series of data presented so far implies that we have been considering here one of those major variations such as have been thought to characterize the period 1920–22 and the early years of the century. For all three periods there have been numerous notes of unusual biological occurrences in various parts of the North Sea and the English Channel, together with records of unusually high salinities and, more or less associated, high temperatures. Evidence drawn from western central North Sea (Shields–Oslo route) and from the Sevenstones Light-vessel (together with the less complete data for the western mid-Channel region), suggest that salinities in the early twenties and the present period were of a similar order; at Varne they were appreciably higher in the earlier period. Owing to the gradual building up of the series of observations it is more difficult to obtain exactly comparable data for the early years of the century, but that reviewed by Lumby for the English Channel (1935) suggests that both near Varne and at the western end of the Channel the salinities were roughly of the same order in 1903–05 as in 1920–22; those in the North Sea do not appear to have differed greatly.<sup>1</sup>

<sup>1</sup> Whilst it might be premature to do more than point to certain similarities in these variations, it may be worth while, in relation to the latest cycle, to draw attention to the recent estimates made by Iselin (1940) regarding variations in the strength of the Gulf Stream System. Briefly, his evidence suggests that during the years 1926–31 its transport was mainly above “normal,” whilst after 1931 and up to 1939 it was mainly below normal. The details of his estimates, however, make it seem reasonable to suggest a connection between the generally decreasing Gulf System transport from 1931–37, followed by an increase (Iselin, 1940, fig. 25), and the generally increasing Atlantic influence in local waters (as judged by salinity) from 1931 to 1935, followed by a decrease. Since Iselin has demonstrated that decreased transport in the central system may permit an increase in the area of the eastern North Atlantic covered by the warm and saline discharge (and *vice versa*), it may be reasonable to expect first increasing, and then decreasing, salinities in European waters during these years. It is also suggestive that Iselin’s evidence provides lower values for the Gulf System transport in the early twenties than after 1925, as might be expected on the grounds of this analogy if the high



Such major cycles are of interest and must have considerable significance for the inhabitants of these waters. It will be remembered that during the period 1932-37 certain trends were found in the abundance of various plankton forms (Lucas, 1940; Rae and Fraser, 1941; Henderson and Marshall, 1944; and



TEXT-FIG. 12.—Showing for certain routes and for the Varne Light-vessel the overall trend in the frequency of salinities exceeding  $34.99\text{‰}$ , excepting in Route 15 ( $35.29\text{‰}$ ), during the period 1930-37 (obtained by the method of moving averages).

Stubbings, in the press), and this biological evidence will be discussed in relation to the hydrological in Part II. The present data, however, may be analysed further, and it is important to discover, if possible, the manner in which so large an area, subdivided by the narrow Straits of Dover, became flooded with high salinity water at the surface (and presumably beneath it).

salinities for the early twenties in local waters truly resembled those of the present period in their derivation. There is at least some evidence, in fact, for what might otherwise have merely been guessed, *i.e.* that such changes as we are considering are likely to have originated in variations of the Gulf Stream System.

*Origin of the Salinity Increases.*

The normal, or rather, the mean, annual sequence of events in surface local waters is presented in the 'Atlas de température et Salinité,' published by the Conseil Permanent (1933) and in Lumby's more detailed review of events in the English Channel (1935). In contrast, the data shown in figs. 2-9 present details of certain events for a particular set of years, apparently comprising part of a cycle. The 'Atlas' shows that the chief annual changes are in relation to influences from (1) the north-west, whereby high salinity water attains a mean maximum extension in the north-western North Sea in the early spring, and (2) the west, whereby high salinity water entering through the English Channel has its mean maximum spread in the south-eastern North Sea, *via* the Straits of Dover, at the end of the year. (3) In association can be seen the Baltic influence producing a mean maximum spread of low salinity water in the summer, as well as the influences of other sources of fresh water. Long term changes over a period of years may be expected to arise rather similarly and, in the case of increasing salinities, we may look for either variably increased penetration from the north towards the Southern North Sea, or higher Channel salinities leading to the flow of more saline water through the Straits of Dover. In view of the relative sizes of the northern and southern openings to the North Sea and the effects exerted through them (see discussion by Carruthers, 1935), it may seem that the former would be the controlling influence in the area at any time, and this receives support for the present period in the evidence of Tait (1935) that there were unusual increases in this influence during the period 1930-34, followed by a decline. There can be little doubt that this influence extended well beyond the mean annual limits, and almost certainly it would increase the salinities along Routes 33 and 32 at least. Further south in the North Sea the nature of the effects are less certain. There have been no accounts of major changes in the English Channel data during the period (other than phosphate), but the evidence provided here for such changes, together with the known annual variations and the not dissimilar changes in 1920-23 and 1903-05, demands that the possible effects of influences from this quarter should also be considered. In association we should review the changes known to occur in the speed and direction of the current at the Varne Light-vessel in the Straits of Dover, since it is commonly held that the water movements in this region reflect, as a buffer, the relative influences exerted from the north and west (Carruthers, 1935).

The current observations at Varne have been made continuously since 1926, the earlier ones being published in full (Carruthers, 1935), and later ones being circulated to various laboratories (see references in Carruthers, 1935, 1938 and 1939) in a most convenient summarized form. We are greatly indebted to Dr. Carruthers for the provision of these data up to the outbreak of war. The data for the years under review are shown here in Text-fig. 11 in the form of monthly records of speed and direction, for comparison with the salinity data, etc. In the years prior to 1930 the directions of the current at Varne were largely east



of north, and they remained so until mid-1931. Thereafter there was a variable but considerable westerly component in them until the end of 1937, so that the major periods of current consistently east of north were the autumn and winter of 1932-33, the spring and summer of 1934, the autumn and winter of 1935-36, and the winter of 1936-37. In 1938 and 1939, however, conditions were such that the current was almost continuously well to the east of north, so that there appears to have been an irregular cycle of current variation. Carruthers (1935) has shown that from 1926 until the middle of 1931 there were usually currents flowing directly, with variable speed, into the North Sea for the greater part of each year; it appears that the same must have applied to 1938 and 1939. Whilst it is probable that for the short periods mentioned above there were also such currents flowing from the Channel, in between them were recorded periods of very different flow, which Carruthers suggests can be interpreted as including periods of "hold-up" or "reversal": among his examples are February and June, 1932. There remain long periods in which the currents were between these extremes and which are more difficult to interpret, since at Varne they were directed towards the English coast and must subsequently have turned differently. However these may have been, the resultant flows within the North Sea must have been different from those following currents with a strong easterly component.

The changes in the direction of the Varne current led Carruthers to consider whether at times the "normal" flow from the Channel might be reversed, and water move into the Channel from the North Sea, presumably with important effects on the local flora and fauna. In particular, he has considered whether the relatively high English Channel salinities of 1922, in relation to those of 1923, may not have been "controlled by Atlantic influences exerted *via* the North Sea," since the mean current at Varne in 1922 was 4.8 miles per day but only N. 25° W., whilst that for 1923 was more "usual" at 3.4 miles N. 23° E. In agreement with the view expressed by Le Danois, he reached the opinion that such North Sea influences can occur, and that they must have been the explanation of the occurrences in 1922. On the other hand, Lumby (1925*a*) could find no contemporary evidence of such a towards-Channel flow of high salinity water in 1920-23 and (1925*b*) opposed Le Danois' opinions. As Carruthers fully realized, Lumby's evidence was "a real stumbling block," and one would expect that the usual effect of any flow from the North Sea would be a reduction in the salinity of the eastern Channel water. The present period presents several similar aspects: again we have years of high Channel (and Southern North Sea) salinity associated with relatively western Varne flows, preceded and followed by years of less salt water associated with easterly flows. Just as he believes happened in 1922, Carruthers also suggests the possibility of such northern control in 1933 (and probably later, by implication), ascribing the unduly westerly flow "to the existence of an extra strong southward thrust of water through the North Sea consequent upon extra strength on the part of the parent Atlantic stream north-west of Scotland" in 1933. In view of the very long period of westerly

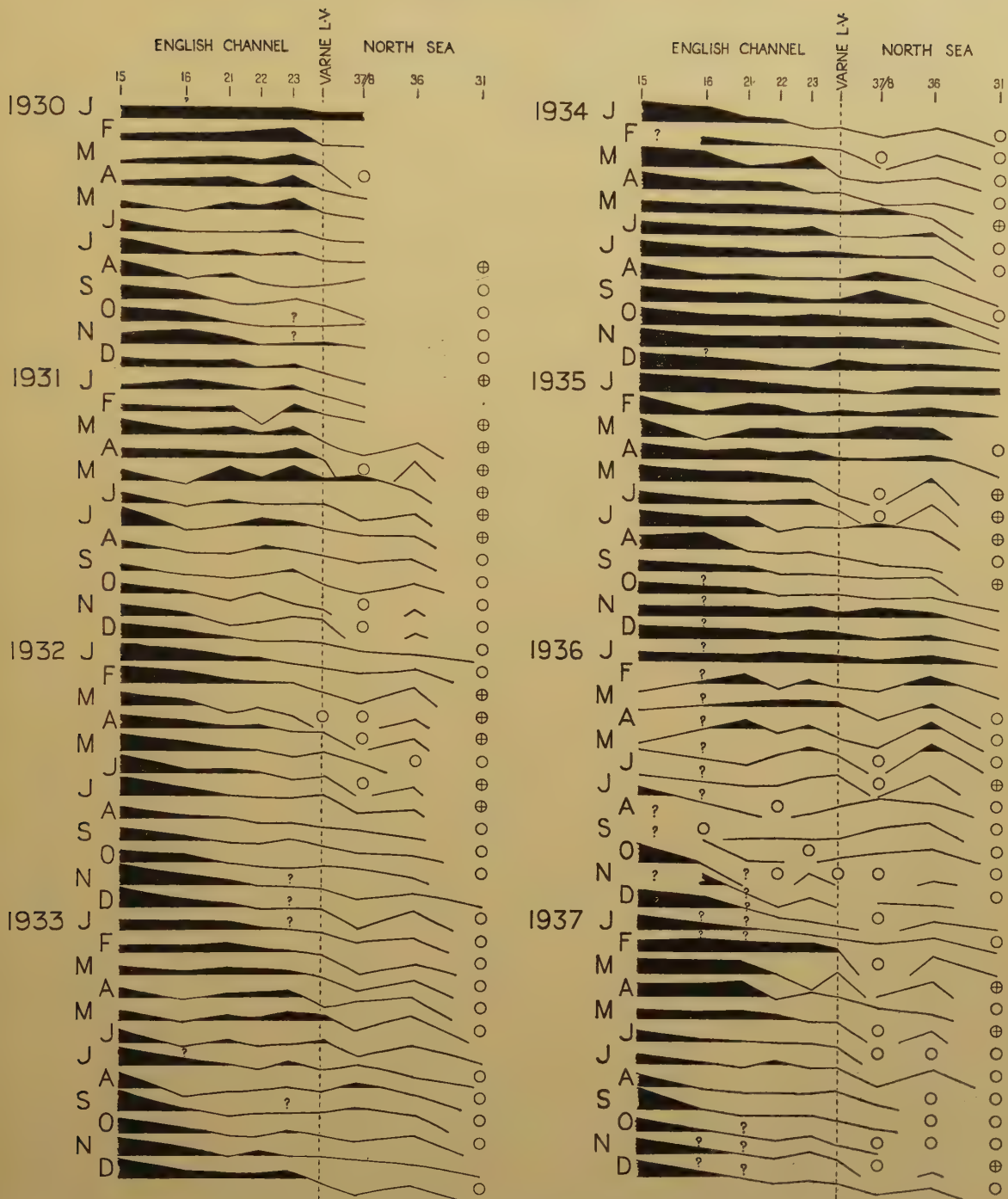
deviation in the Varne flow, it is necessary to decide here how far the high salinities in the Southern Bight and eastern Channel may have been largely the result of such northern influences.

Again there appears to be the immediate objection to this hypothesis that in general the salinities recorded at the surface decreased from Route 33 to Route 32 and then to Routes 31 and 36 (except during the period autumn, 1934, to spring, 1936, in which higher salinities were found on these lines than were usually to be found on Route 32). The combined Routes 37 and 38 show yet higher salinities, usually of the order of those found in the eastern Channel, whilst the salinities further west in the Channel were usually higher still. It would thus appear that at the surface there was no continuity of high salinity water through the series of Routes 33, 32, 31 and 36 to 37-38 (*i.e.* moving further south in the North Sea). There would, however, appear to be general continuity through the series starting at the western end of the Channel and moving through the Dover Straits to Routes 37-38, 36 and 31. This is shown more clearly by consideration of Text-fig. 13, showing the mean monthly salinities for a series of selected stations starting at the western end of the Channel and moving towards Varne and then into the Southern North Sea (see p. 10 and Text-fig. 1). Whilst there are occasional breakdowns in continuity (*e.g.* on the station from Route 16, doubtless due to local production of brackish surface water), there appears to be a fairly continuous high salinity stream, directed towards the North Sea, of a very varying extent. Salinities exceeding  $35^{\circ}/_{\infty}$  extended only for a short distance up Channel, for example, in the autumn of 1931, whilst in the winter of 1934-35 there was a more or less continuous region of water well above  $35^{\circ}/_{\infty}$  extending right through the Dover Straits and partly along Route 31.<sup>1</sup> Between these more or less continuous stretches of salter water and the high salinities of Route 33 there were, as far as our data go, always appreciable regions of lower salinity water at the surface. To this extent it would appear as though the high salinity water of the Southern Bight originated from the Channel rather than from the north-west, and this would apply even more to the waters of the eastern Channel.

Such a suggestion is open to the immediate objection that the surface values may not be fairly indicative of the waters in the various regions, despite the general evidence reviewed above (p. 3) that they do not "normally" show great differences from the rest of the water column (particularly in the autumn and winter when there were very high salinity values). There are reasons for thinking that this period is not a "normal" one, and we must examine such evidence as there is regarding the possibility that the higher salinity waters of the Southern Bight (and eastern Channel) may have originated in the *deeper* water to the north. If we omit the unlikely possibility that high salinity water may have come to Routes 31 and 36-38 from the sub-surface waters of the eastern side of the North Sea (for which there is no evidence), we are left with the western waters of the

<sup>1</sup> The great extent of the from-Channel water exceeding  $35^{\circ}/_{\infty}$  in January, 1935, has already been demonstrated by Kunne (1935) and Kalle (1937).





TEXT-FIG. 13.—Showing for the years 1930–37 the mean monthly salinities along a series of the standard stations approximating to the route taken by water flowing along the English Channel, through the Straits of Dover, and into the North Sea (see Text-fig. 1). The Route numbers are given above whilst graphs and symbols are used as in Text-figs. 2–9,

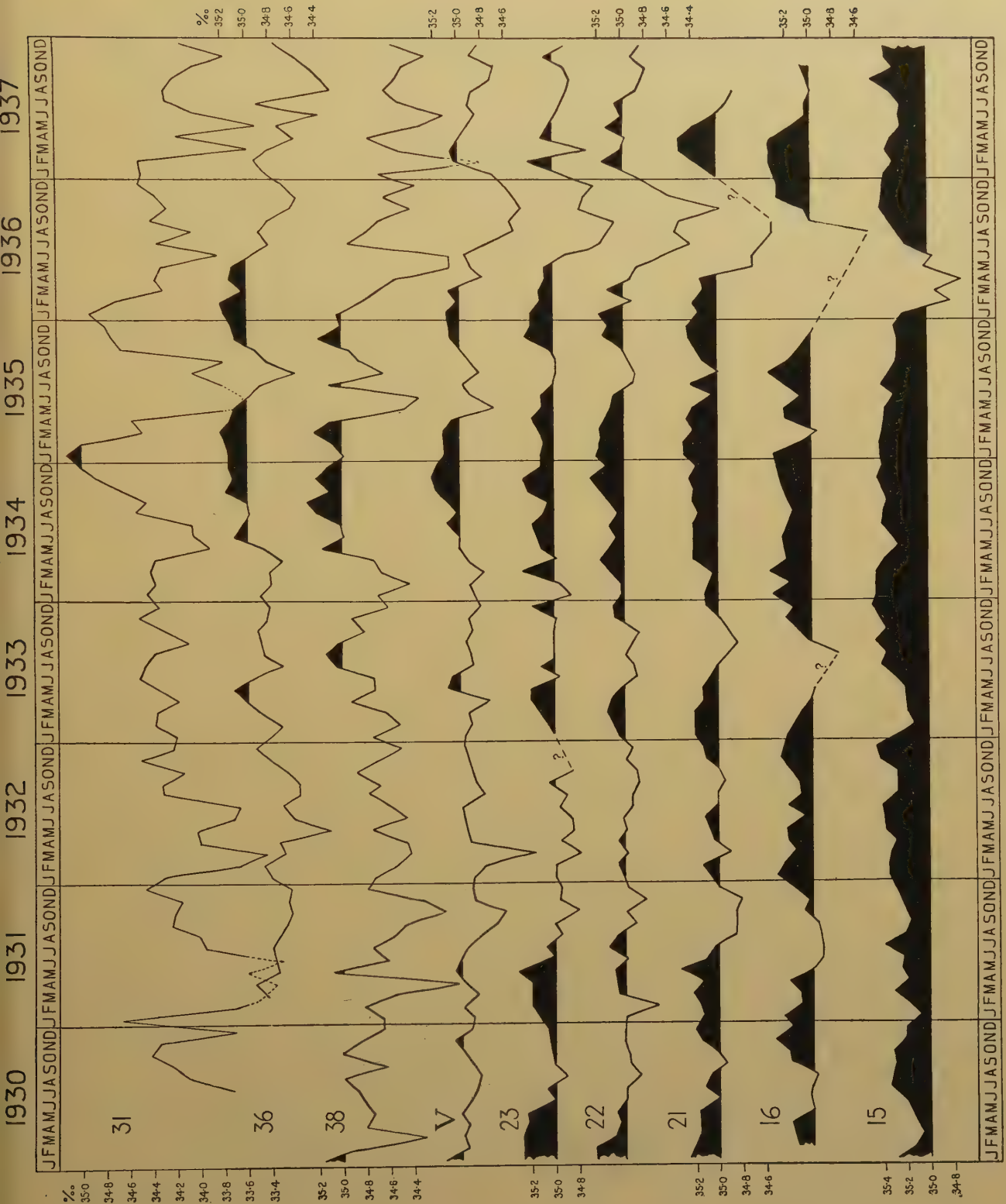
"Gateway" between the Dogger and the English coast, which are necessarily the more likely. Fortunately, there is direct evidence regarding these from the series of stations off Flamborough Head investigated in 1933 and 1934 by Savage and Wimpenny (1936), and also along a line through the "Gateway" in 1934 and 1935 sampled by Graham (1936) and Graham and Harding (1938). These strongly suggest that rarely, if ever, in those years was water to have been found in the "Gateway" of sufficiently high salinity to account for the high values recorded regularly on the routes of the Southern Bight. When taken with the evidence that regularly, and approximately at the same times, there were suitable salinities to be found in continuity to the south and west of these routes, we are forced to the conclusion that not only the high salinities of the eastern Channel water, but usually those of the Southern Bight as well, must have originated from the west, *via* the Straits of Dover.<sup>1</sup> This is confirmed by the alternative presentation of the data from Text-fig. 13 in Text-fig. 14, where undoubted trends towards the North Sea of both high and low salinity water can be seen much more clearly than in the reverse direction. There still remains every reason to believe that the relatively high salinities of Route 33, probably most of those along Route 32, and possibly some recorded at the western ends of Route 36 (p. 15) did, in fact, derive from further north in the North Sea. So far, however, from the more southerly of these having contributed towards the increasing salinities in the Southern Bight in 1933-36, they were more likely, owing to their lower salinity, to cause dilution of the more southern waters if mixing occurred.

Thus the evidence for spatial continuity of high salinity water (and, it will be seen, of low salinity water) points, even for this exceptional period, towards the conventional picture of the relations between the western and the north-western influences (p. 24). The question then arises of how, during years in which the northern pressure increased and the Varne current deviated so much to the west that Carruthers was led to postulate hold-up or reversal, surface water of unusually high salinity came to flow from the Channel in quantities sufficiently large to produce increases in salt content over the Southern Bight which were sometimes higher than contemporary values as far north as Route 33. Such an apparent disagreement makes it necessary to consider in more detail the relationships between the Varne current and the movements and salinity of adjacent waters. How, in fact, are the indications of current *direction* at Varne to be interpreted?

This point will be considered in more detail in relation to our plankton data, but it may be well to indicate now the type of problem raised here. In Text-fig. 11 there is shown the average degree of penetration of the salter water along Route 31 (*i.e.*, from the more southerly station I to the more northerly station V, see inset chart), in relation to the varying Varne flow as recorded by Carruthers. As we have seen above, there was no agreement between the general degree of easting and westing of the current, and the general extent of higher salinity water. On the

<sup>1</sup> Here, in fact, appears to be the origin of the high salinities recorded in 1934 by Savage and Wimpenny (1936, p. 22).





TEXT-FIG. 14.—Showing for each of the stations used in Text-fig. 13 the mean monthly salinity variations during 1930-37. The scales used for the stations are indicated alternately at the sides of the graphs, salinities exceeding 34.99 ‰ being blacked-in.

other hand there was still a surprising degree of similarity in *phase* between *changes* in the two factors (just as Carruthers has shown similarity in phase between the *changes* in speed and direction, see also Text-fig. 11). *Relative easting* tended to associate with or to be followed by apparent movement *along* the route of relatively (but not always actually) higher salinities, and *vice versa*. This type of relationship is seen over a wider field if we consider the data of Text-fig. 13, together with the current directions shown in Text-fig. 11. Again the spread of salter water was usually associated with *relative easting* (*i.e.*, veering currents), although similar amounts of easting were seldom associated with similar salinity distributions. On the other hand, what appeared to be steadily developed tongues of salter water at the surface were, often suddenly over a wide area, diminished in extent and saltiness after times of *relative westing*. The significant feature again appears to be the *relative* nature of the changes at any time (*i.e.*, veering or backing). In connection with this, it is significant that, when comparing Varne currents at the normal depth of  $6\frac{1}{2}$  fathoms with some recorded specially at  $12\frac{1}{2}$  fathoms, Carruthers found a mean directional difference of  $21^{\circ}$  E. at the greater depth, the deeper current being more easterly for eleven occasions out of fifteen. If these interpretations are correct, then the significance of the less easterly and the westerly currents may require very careful interpretation. By no means always and possibly seldom are they indicative of a reversal of flow, although they would certainly appear to indicate important changes in the local conditions.

One other instance may be given of the uncertain nature of their interpretation on their own evidence—one concerning the arrival of water of unusually low salinity in the region of the Varne Light-vessel (Text-figs. 10, 13 and 14).

Text-fig. 10 shows that salinities exceeding  $35.29^{\circ}/_{\infty}$  decreased on Route 15 during the second half of 1935 and remained very low well into 1936. Similarly there was a period of low salinity on Route 22 in 1936, and further "troughs" in the salinity curves can be seen in turn on Route 23 and then at the Varne. These are seen in Text-fig. 13, and in Text-fig. 14 showing the same data plotted against time on the horizontal scale. Unduly low salinities appeared near the centre of Route 15 in February, 1936, and on Route 21 in May. On Route 22 they first appeared in June, and on 23 in July, whilst at Varne the first remarkably low sample was found in August. Unfortunately certain samples are missing from the mid-stations of Routes 16 and 21, so that the arrival at the first and the disappearance from the second position is not clear in Text-fig. 14: there seems every reason to suppose that they were intermediate in both instances between the preceding and the following routes. We see, then, the appearance and disappearance of this unusually brackish water route by route, and it must have progressed steadily up Channel, persisting some six or seven months at each of the stations up to and including Varne. The first appearance of truly low salinity water on Route 15 coincided with backing of the flow at Varne, followed in April and May by very westerly currents, and then moderate but variable ones from June to October. By May this water had arrived on Route 21, and by June on Route 23,



at least; by July it was apparently at Varne. Good estimates of the extent of this "patch" can be seen in the relevant figures, and it seems to have spread from side to side of the Channel at times, and to have extended for well over 100 miles on the surface.

This is presumably the patch recorded by Dr. Harvey in 1936 (see Kemp, 1938). In spite of the frequent westerly current directions at Varne, it moved at a fairly steady pace up Channel, covering the first half of the journey in roughly the same time as the second. On the other hand, of course, the arrival of such water at the eastern end of the Channel, and its apparent passage through the Straits, completely displaced the previously continuous stream of higher salinity water apparently stretching as far as Route 36. The important thing, however, appears to be that not only was there a from-Channel flow, for example, in the winter of 1935-36, in association with quite easterly currents, but that even whilst the current was moving back as far as  $32^\circ$  and  $45^\circ$  west of north (April and May, 1936), the Channel was first receiving, and then conveying, a readily detectable body of water, some of which was to reach (and possibly pass) Varne before the onset of the more easterly flows of the autumn. During this time there were only two months of flow to the east of north at Varne (although the speeds in 1936 were relatively high). The passage of other low salinity patches can be seen in Text-figs. 13 and 14.

It would appear as if with all but the extreme westerly currents there was still a from-Channel surface flow which, at times when the Varne current was tending more towards the west, was "hugging" the English coast rather than the continental one.

#### SUMMARY.

1. In order to provide a hydrological background for the continuous plankton records of 1932-37, the regular International Council surface salinity observations over a series of routes in the central and southern North Sea have been reviewed for 1930-37, together with some from the English Channel.

2. Each route shows its individual features and seasonal variations, but all are agreed in showing a salinity cycle, with maximal salinities during the winter of 1934-35. Others have also reported a similar cycle for the Northern North Sea in association with waxing and waning Atlantic influence. Representative trends of the decreasing and increasing proportions of salter water suggest a fair uniformity in this cycle over the whole area, and it may be compared with similar changes during the periods 1920-22 and 1903-8. A possible connection with variations of the transport of the Gulf Stream system is mentioned.

3. The possible origin of such a salinity increase is discussed, and the evidence suggests that while increases in the central North Sea must have derived largely from the north, the major increases in the Southern Bight and the Eastern English Channel must have arrived from the western end of the Channel in association

with streams of unusually salt water which frequently penetrated well into the Southern North Sea.

4. The question is then raised of how, at times of increased northern penetration and unusually westerly Varne flow, such salt water passed up the Channel. It is known that deeper currents may be more easterly than those at the depths normally measured at Varne, and the present evidence, including that for the steady passage up Channel of a large patch of less saline water, suggests that only the most extreme westerly Varne currents may indicate hold-up or reversal.

5. The data will be discussed further in relation to the plankton records in Part II.

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# INVESTIGATIONS INTO THE FOOD OF THE COD (*GADUS CALLARIAS* L.) OFF BEAR ISLAND, AND OF THE COD AND HADDOCK (*G. AEGLEFINUS* L.) OFF ICELAND AND THE MURMAN COAST

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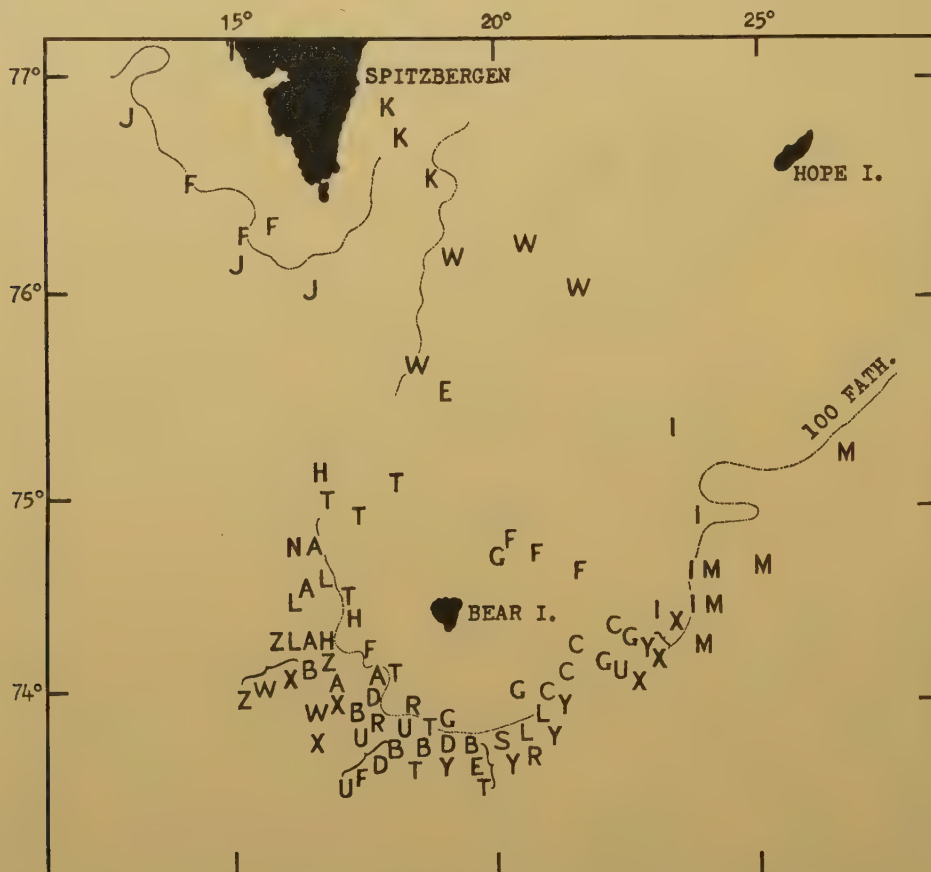
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## INTRODUCTION.

The fishing grounds off Bear Island in the Barents Sea have been exploited (except during the war) by British trawlers, mainly from Hull and Grimsby, since 1928, and were found to be very prolific. The catch is almost entirely of cod (*Gadus callarias* L.)<sup>1</sup>



TEXT-FIG. 1.—Chart showing the positions of trawl hauls from which samples of cod stomachs were taken in the Bear Island and Spitzbergen fishery, 1936–38. The letters refer to the different voyages; their dates will be found in Table I.

Observations on the food of the Bear Island cod had been made by the Russian investigator V. A. Brotsky in 1930, giving data for all months of that year except February, March, May and September (in Zenkevich, Brotsky and Dektereva, 1931), and by the late Mr. J. A. Robertson, of the Ministry of Agriculture and

<sup>1</sup> Other commercial species taken are Haddock (*G. aeglefinus* L.), Coalfish (*G. virens* L.), Soldier (*Sebastes norvegicus* L.) and the Spotted catfish (*Anarrhichas minor* Olafsen); among non-commercial species the more frequent are the Long Rough Dab (*Drepanopsetta platessoides* O. Fabricius) and Blue Catfish (*Anarrhichas latifrons* Steenstrup).



Fisheries, who made a voyage there in a trawler in July of the same year (Robertson, 1932).<sup>1</sup>

In August, 1936, Mr. G. C. Trout, now on the staff of the Ministry of Agriculture and Fisheries but then a student, collected nearly 200 preserved cod stomachs on a voyage to Bear Island on a Hull trawler; these and other samples which he collected later he has kindly placed at our disposal for analysis with our other material. One of the present authors (W. W. Brown), who had made another voyage to obtain data in December, 1936, began a more detailed study as a post-graduate student at Hull in the following summer. He wishes to acknowledge aid from a Frank Parkinson Scholarship of the University of Leeds. It was clear that one worker could not obtain all the samples and in a limited time

TABLE I.—*Dates and Numbers of Cod Stomachs obtained on Various Voyages to Bear I., Spitzbergen Bank, Murman Coast, Andanes and Iceland during 1933, 1936, 1937 and 1938.*

| Locality.         | Voyage.          | Month and year.             | Total number of stomachs. | Number of stomachs containing food. |
|-------------------|------------------|-----------------------------|---------------------------|-------------------------------------|
| Bear Island       | C                | . Aug. 26–Sept. 1, '36 .    | 198                       | . 198                               |
|                   | B                | . Dec. 24–Jan. 3, '36–'37 . | 100                       | . 59                                |
|                   | A                | . May 13–21, '37 .          | 46                        | . 30                                |
|                   | D, E             | . Sept. 4–18, '37 .         | 89                        | . 87                                |
|                   | F, G             | . Oct. 25–31, '37 .         | 22                        | . 15                                |
|                   | F, G, H, I, M    | . Nov. 1–28, '37 .          | 146                       | . 110                               |
|                   | L, M, N, O, P, T | . Dec. 1–31, '37 .          | 71                        | . 42                                |
|                   | Q, R, S, T       | . Jan. 1–27, '38 .          | 90                        | . 56                                |
|                   | S, U, W          | . Feb., 5–28 '38 .          | 20                        | . 16                                |
|                   | W                | . Mar. 1–4, '38 .           | 5                         | . 2                                 |
|                   | X, Y, Z          | . Apr. 12–30, '38 .         | 32                        | . 28                                |
|                   | X                | . May 1–4, '38 .            | 5                         | . 3                                 |
|                   | Total            |                             | 824                       | . 646                               |
| Spitzbergen Bank  | F, J, K          | . Oct. 26–Nov. 25, '37 .    | 55                        | . 27                                |
| Murman Coast      | M                | . Dec. 29–Jan. 5, '36–'37 . | 90                        | . 90                                |
| Andanes (Andø I.) | S, V             | . Jan. 29–Feb. 23, '38 .    | 51                        | . 16                                |
| Iceland           | A                | . Aug.–Sept., '33 .         | .. <sup>2</sup>           | . ..                                |
|                   | B                | . Aug. 4–13, '36 .          | 76                        | . 76                                |
|                   | C, E, F          | . June 1–30, '37 .          | 86                        | . 70                                |
|                   | D, F, G          | . July 2–31, '37 .          | 46                        | . 36                                |
|                   | G                | . Aug. 3–10, '37 .          | 49                        | . 49                                |
|                   | Total            |                             | 257                       | . 231                               |
|                   | Grand total      |                             | 1,277                     | . 1,010                             |

<sup>1</sup> See also Zatsepin and Petrova (1939) for observations in the Barents Sea. Owing to wartime conditions attention was not drawn to their paper until this one was in the press.

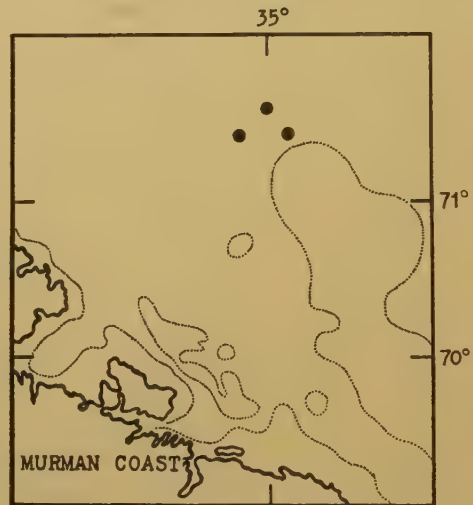
<sup>2</sup> The material from this voyage is not included here, or in the general discussion, since we have no records of the actual numbers of stomachs examined (see p. 49).

carry out their analysis. The collection of further material was made with the generous help of a number of skippers of trawlers belonging to Messrs. Hudson Brothers Trawlers Ltd., of Hull, who each undertook to preserve samples of cod stomachs in accordance with instructions provided. Mr. A. Hudson had very kindly given permission for them to be approached.

The sampling had no sooner begun in May, 1937, when a Government ban on the landing of fish from the far northern grounds prevented more material being collected from Bear I. till early in September. From then until the following May, when the ban was again imposed, there was a continual supply of samples



TEXT-FIG. 2.—Position off Andø I. (marked X) from which samples were taken, Jan. 29th–Feb. 23rd, 1938.



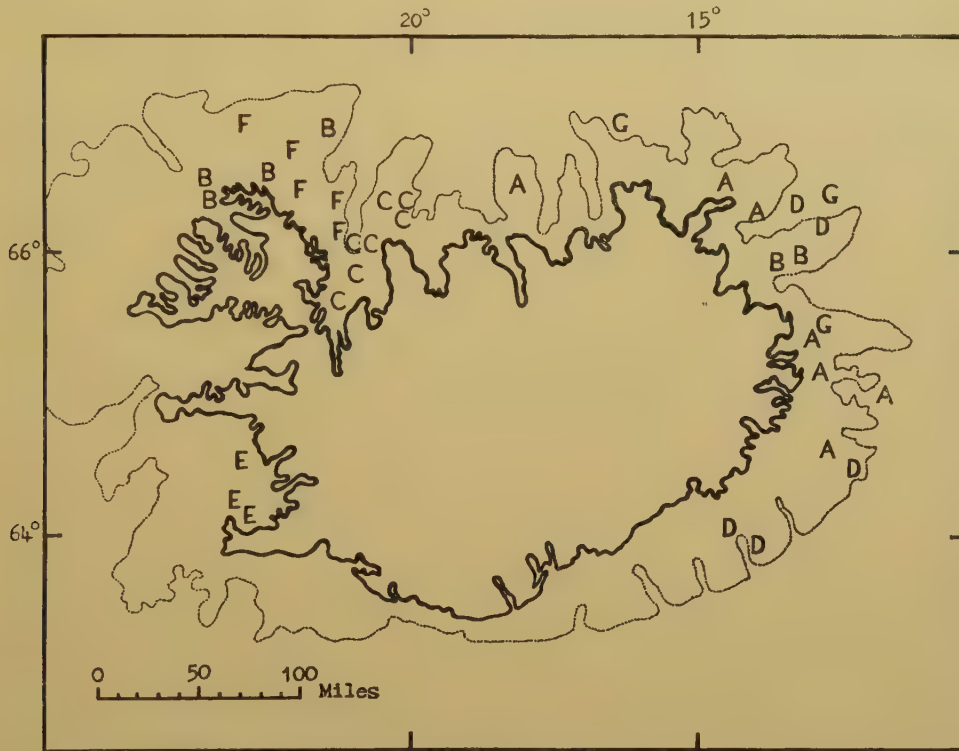
TEXT-FIG. 3.—Positions from which samples were taken off the Murman Coast, Dec. 29th, 1936–Jan. 5th, 1937.

obtained on 24 voyages. It is fortunate that the unavoidable absence of data for June and July in our records is compensated for by the observations of Brotsky and Robertson for those months in 1930, and that our own records in turn compensate for the gaps in Brotsky's records for February, March, May and September. The two sets of data, which we shall later review together, provide a general picture of the feeding of the cod at Bear I. throughout the year.

Bear Island (Björnøy) lies in Lat.  $74^{\circ} 30' N.$ , Long.  $19^{\circ} E.$ , roughly midway between North Cape, the most northerly point of Norway, and Sar-Kap, the southern tip of Spitzbergen. It is in the centre of the south-western projection of the Spitzbergen Bank, the 100 fm. line from the E. round the south of the Island to the N.W. roughly following the coastline at a distance of 20–35 miles. The bank is divided from the coastal bank of Spitzbergen by an inlet of deeper water, the Gulley-way.

The island stands at a point where the Arctic currents meet and mix with the north-eastern arm of the North Atlantic Current (continuation of the Gulf Stream) which keeps the sea to the south and west free from ice throughout the year. The ice, however, prevents operations on the edge of the Gulley-way in January and February, and sometimes into March or even later.

The bottom, both round Bear I. and on the Spitzbergen Bank, is almost uniformly of fine sand, mud and shell, and can thus be worked with a trawl over all its area.



TEXT-FIG. 4.—Chart showing the positions of trawl hauls from which samples of cod stomachs were taken from the Iceland fishery in 1933 and 1936–37. The letters refer to the different voyages, the dates of which are given in Table I.

Some of the hauls included in this investigation are from Spitzbergen Bank, where the fish taken are the same as at Bear I.<sup>1</sup>

Text-fig. 1 shows the approximate positions of the hauls from which food samples were obtained in the Bear I. and Spitzbergen region. The letters indicate the different voyages made, and the dates for these will be found in Table I on p. 37.

<sup>1</sup> At times the cod from Spitzbergen have a strong and unpleasant flavour of seaweed, which, although it has no ill effects on the consumer, lowers its market value so considerably that skippers will not fish there. During the period of these investigations, however, the fish from Spitzbergen did not show this contamination, and a number of trawlers worked there until the ice came down towards the beginning of December.



In February and March many of the boats which usually fish at Bear I. work off Andanes, on the island of Andö, at the northern end of the Lofoten Islands (see Text-fig. 2). There is here a narrow bank, close to the coast, which is used as a spawning ground by the cod, and is also frequented by haddock at this time of the year. Hauls are included from here to show the diet at the time of spawning.

On all these grounds the fish are taken almost exclusively on the edges of the banks, in depths of 60 to 210 fms. The gear used is the large otter trawl, with the doors separated from the wings by ground cables. This sweeps a large area of the bottom, and not uncommonly may catch up to 300 baskets per hour's fishing (each basket holding 5-6 stones).

During the months of June, July and August, 1937, when the trawlers were prevented by the ban from going to Bear I., samples of cod stomachs were collected on seven voyages to Iceland. Mr. Trout had also made collections from Iceland in the August of 1936, and on a voyage to the Murman coast in January, 1937. The samples from all these voyages are included and the positions of the hauls are shown in Text-figs. 3 and 4.

The present report is based mainly on the examination of 1277 cod stomachs, of which 1010 contained food. As will be explained under sources of error, the method of collection limited the material to the food of smaller cod, full-sized stomachs being too large for the sampling jars used. In addition, Mr. Trout on the two last voyages mentioned collected haddock stomachs—40 from Iceland and 137 from the Murman Coast. Since they were taken in the same hauls as the cod their contents are also described, and provide some material towards a comparative study of the feeding of the two species. Some samples of cod food brought from Iceland in 1933 (voyage A, Table I and locality A, Text-fig. 4) are not included in the data used in the general discussion, as we have no records of the actual number of stomachs examined; the occurrences of the various food organisms found in them are, however, included in Appendix II.

The first author (W. W. B.) having worked through and sorted all the material into groups and identified many of the more important organisms, including the fish and euphausiaceans, was unable to complete the work before being mobilized with the Territorial Army at the outbreak of war in 1939. As a preliminary to further research in northern waters after the war, the Fishery Advisory Committee of the Development Commission expressed a wish in 1944 that the work should be completed, and with his (W.W.B.'s) approval the second author (C.C.) was appointed, with a grant from H.M. Treasury, to undertake the completion of the analysis and the writing of the report.

We most gratefully acknowledge the help given in the collection of samples by the following trawler skippers: C. Agerskow, C. Burroughs, G. Carrill, F. Dale, J. P. Grantham, J. Mann, G. Matthews, H. Sanderson, and T. Threlfall; by Mr. G. C. Trout, mentioned above, who also made three voyages for us; and by Mr. L. D. Renouf, who made a voyage to Bear I. in September, 1937. The first author

made voyages to Bear I. in December, 1936, and September, 1937, and to Iceland in August, 1937.

Assistance in the identification of specimens will be acknowledged in the appropriate sections to follow.

## METHODS AND IDENTIFICATION.

### *Method of Collection.*

The trawlers were provided with boxes divided into eight compartments, into each of which fitted a three-pound screw-topped jar. The jars were held tightly, when the box was closed, by felt linings on the bottom and lid; this was very necessary, as the boxes were subjected to a good deal of heavy movement in the long period of bad weather experienced.<sup>1</sup> The jars were clearly numbered on the lids from 1 to 8, these numbers corresponding to eight numbered pages of the note-book placed in each box. Each page had spaces to be filled in by the skipper giving the following particulars: *Date, Time, Approximate position of the haul, Depth of water, Catch in baskets of cod, sprags<sup>2</sup> and codling, and Weather conditions.*

Each skipper was provided with a sheet of instruction, of which the following is a copy:

### UNIVERSITY COLLEGE OF HULL: COLLECTION OF FISH FOOD FROM NORTHERN WATERS.

We have now begun a study of the food of the cod in Northern waters, and shall be very grateful for the co-operation of trawler skippers in obtaining samples for us. We have already examined a number of samples from Iceland, Bear Island and the White Sea, and these show that the food taken by the cod varies very greatly in different places and at different times. It is hoped that we shall, in time, know more about the habits and movements of the fish from a study of their feeding habits in different areas, and at different seasons of the year.

A box containing 8 screw-topped jars is provided, each jar being half full of preservative fluid (Formalin). When the fish are being gutted, we should like the stomachs from as many fish as will fill it to be dropped into a jar, each jar being used for a separate haul. They should, if possible, be spaced out in the voyage to give samples from as wide an area as possible, *e.g.* if it is expected that some 40 hauls will be made in the trip, then a sample can be taken every fifth haul.

A notebook is provided, with pages numbered to correspond with the numbers of the jar. Thus, as each jar is filled up, the information regarding that haul is recorded under the same number in the book.

At present we require samples of cod stomachs only.

<sup>1</sup> The only time any jars were broken was when a temporary container had to be used because no standard box was available. The only other loss sustained was that of a whole box which, although apparently well lashed, was washed overboard when the vessel received a very severe battering off the Norwegian coast, resulting in considerable damage to the bridge.

<sup>2</sup> Medium-sized cod.

Advance information of the movements of the trawlers was kindly given by Mr. Waltham, Secretary to Messrs. Hudson Brothers Trawlers, Ltd.; the full boxes were exchanged for empty ones while the vessels were in dock between trips.

On the whole the skippers seemed to take a reasonable interest in the work, and took care to see that the material was collected according to instructions. After Christmas the general weather was, unfortunately, very bad and, as was only to be expected, the collections fall away in number. Owing to the extremely arduous nature of the work in these Arctic waters from January to April, with heavy seas, frosts and lack of sleep, it would be unreasonable to expect them to bother about any extra trouble, however slight it might seem to one unaccustomed to the conditions. That we obtained material at all in these months is much to the credit of the skippers concerned, and we are most grateful to them.

#### *Sources of Error in Collection.*

There is one major source of error in this method of sampling. Owing to the small size (3 lb.) of the collecting jars, very large stomachs were almost entirely excluded; to use bigger jars would have meant fewer samples obtained, since there was a limit to the size of box that could be taken. The number of large cod taken at Bear I. is comparatively small (they nearly all range between 50 and 80 cm. in length); but, unfortunately, the stomach of even a medium-sized cod, when fully distended, is of sufficient size to exclude it from the jars. When small animals were being eaten in large numbers, the record was fairly accurate; but if fishes such as adult herring or codling were being taken in any quantity, the distended stomachs were absent from the collection. When, however, large herring were taken in numbers, remains were usually found for some considerable time afterwards in the stomach; usually the scales would lodge in the crevices of the lining. Thus, it is probable that some trace of large herring would be noticed, if any numbers have been taken. On each of his trips the first author found at different times of the year that a small and fairly steady proportion of the fish were taking small numbers of the same species. These, however, are very rarely caught in the trawl, and are apparently scarce; if they were there in larger numbers, they would probably form a higher proportion of the diet. This cannibalism is only to be expected in a fish such as the cod, which is omnivorous and, according to Graham (1923) and Meschkat (1936), will swallow not only living organisms, but anything which comes into its way in the water; he (W.W.B.) has found in stomachs such articles as mutton bones, boiled potatoes, furnace clinkers, and the guts of cod thrown overboard from trawlers.

It should be noted that this type of investigation, depending upon commercial trawlers, cannot provide much information as to whether the fish are feeding on one kind of food when they are present in large numbers, and another kind when they are scarce. When the distribution of the fish is patchy, the trawlers naturally tend to move away from such areas.



*Method of Examination.*

The contents of one jar, representing one haul, were examined at a time. A preliminary note was made of the type of contents and the size of each stomach, and the contents of the whole jar were then sorted and counted. Only such detailed identification as was possible without microscopic examination was carried out at this stage. All contents not identifiable by this preliminary inspection were preserved and labelled for later, more thorough examination. Representative specimens only were preserved of those species which could be identified at this stage.

Since much of the food was in a semi-digested condition, some precautions had to be taken to avoid duplication when counting. In the case of the euphausiaceans, the practice was to count the eyes which usually remain undigested in the stomach, and are easily identified; in the case of the larger crustaceans, the fragments could usually be pieced together, and an accurate estimation of the numbers made. When dealing with disintegrated annelids, the number of heads present were counted. In dealing with fish remains, there was no constant structure to use; for *Gadus* and *Sebastes* the otoliths were useful, whilst with well-digested gadoids and small herring, complete or almost complete vertebral columns were used. Care had to be taken when dealing with fish, since the cod will frequently take smaller fish in the net after being caught. It was assumed, therefore, that any fish in the stomachs, which were absolutely undigested, had been taken after the fish had been caught, and were excluded from the estimate of the stomach content.

*Identification.*

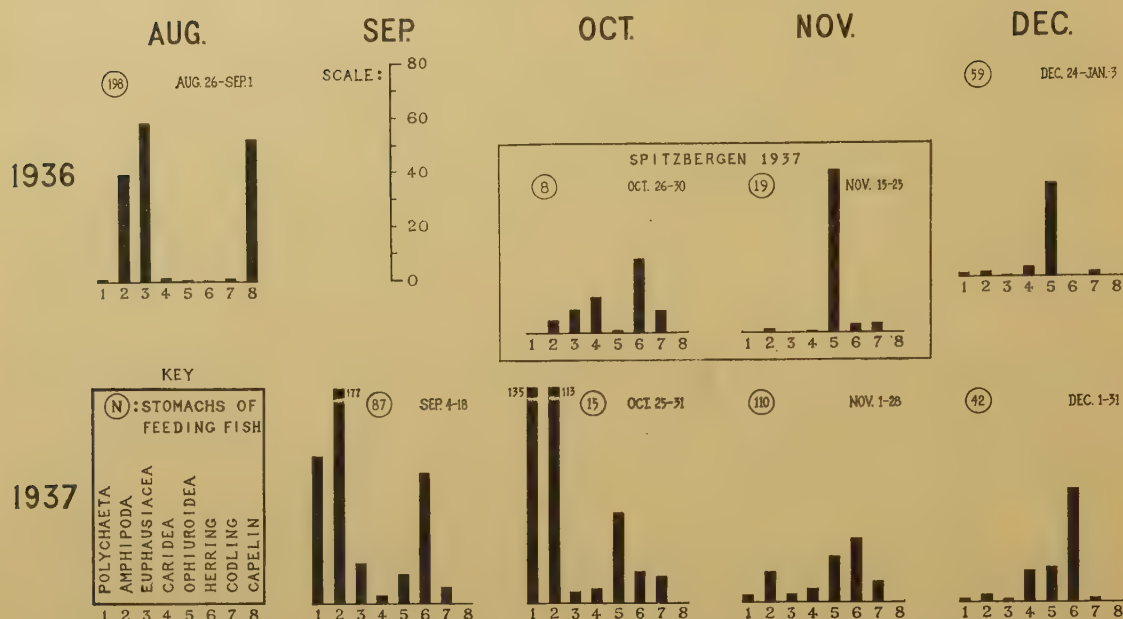
The foregoing notes on the method of examination were written by the first author, who sorted the material into groups and identified part of the Euphausiacea and Hyperiidæ and most of the fish. The remainder of the identifications, were made by the second author, except the Mollusca, Gephyrea and Polychaeta, which were kindly identified by Dr. A. C. Stephen of the Royal Scottish Museum, Edinburgh, and the Actiniaria, by Professor T. A. Stephenson of Aberystwyth, whose report is given in the Appendix I. We are much indebted to them for their kind assistance.

As was only to be expected, many of the specimens were too far digested to allow of accurate identification, particularly in the case of soft-bodied forms, such as medusae, ctenophores and worms. Most of the Crustacea, Mollusca and Echinodermata were sufficiently well preserved, some in nearly perfect condition.

## THE FOOD OF THE COD.

*Bear Island and the Spitzbergen Bank.*

A total of 824 cod stomachs were examined from Bear I., and of these 646 were found to contain food. The dates on which the samples were collected are shown in Table I and their positions in Text-fig. 1.



TEXT-FIG. 5.—Histograms showing the relative numbers of the more important food organisms taken by the cod off Bear Island in different months in 1936, 1937 and 1938, and off Spitzbergen (inset) in October and November, 1937. For comparison all values are expressed as the average numbers taken by ten feeding fish. The actual number of stomachs containing food examined in each month is shown by a number enclosed in a small circle (see Appendix III, Table I).

The number of different species of food organisms identified are as follows :

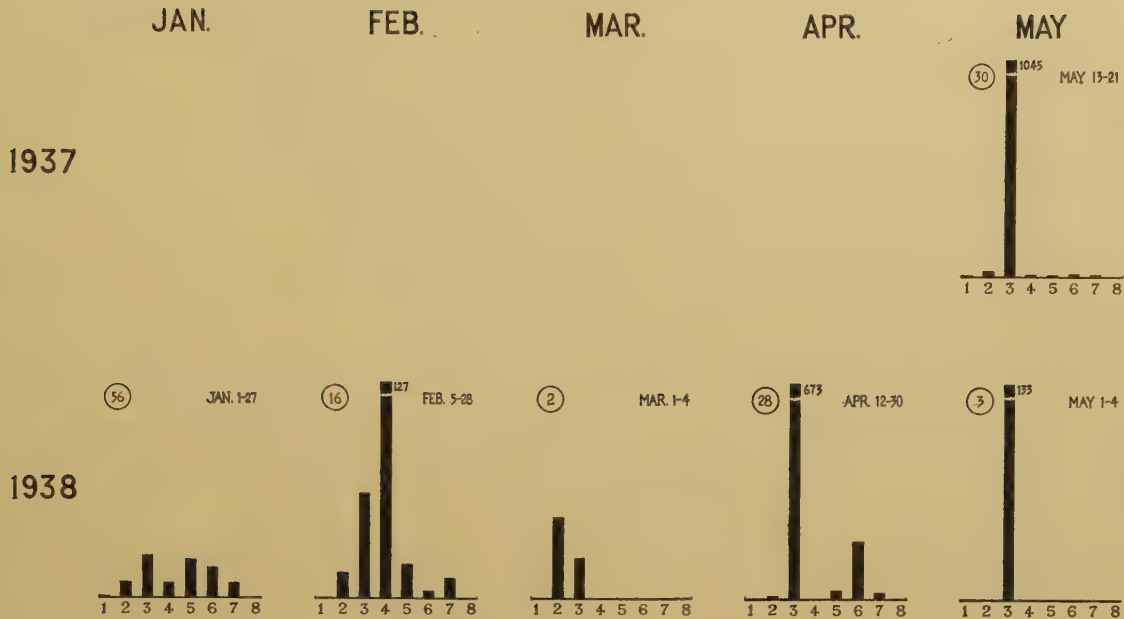
|                       |   |   |   |   |    |
|-----------------------|---|---|---|---|----|
| Actiniaria            | . | . | . | . | 3  |
| Polychaeta            | . | . | . | . | 7  |
| Crustacea             | . | . | . | . | 31 |
| Pycnogonida           | . | . | . | . | 2  |
| Mollusca              | . | . | . | . | 10 |
| Gephyrea <sup>1</sup> | . | . | . | . | 4  |
| Echinodermata         | . | . | . | . | 6  |
| Pisces                | . | . | . | . | 10 |

A full list of the different species with details of their occurrence is given in Appendix II. It will be seen that the majority of species belong to the Crustacea, of which no less than 17 fall into the Order Amphipoda.

The most important food organisms numerically are the Polychaeta, Amphipoda (Hyperiidæ), Euphausiacea, Caridea, Ophiuroidea, Herring (*Clupea harengus*), Capelin (*Mallotus villosus*), and the cod's own young, codling.

Text-fig. 5 compares graphically the varying numbers of these different groups of organisms found in the stomachs in the different months for which we have samples, and Text-fig. 6 shows these seasonal changes, group by group.

<sup>1</sup> Including Echiuridae, Siphunculidae and Priapulidae.



TEXT-FIG. 5 (cont.).

Table II compares our results with those obtained in 1930 by Brotsky (1931) and Robertson (1932). The three sets of data together give a general picture of the main changes in the diet throughout the seasons.

The most striking feature is the importance of the pelagic crustaceans over the greater part of the year—from February to September. In January both Brotsky's and our data show a very mixed diet; in our samples the euphausiacean *Thysanöessa inermis* comes just first in numbers. The prawn *Pandalus borealis* predominates in February, and the pelagic amphipod, *Parathemisto oblivia*, does so in March. From January to March the cod appear only to be feeding casually, and it is doubtful if they exercise any selection. The number of empty stomachs is high, and it is noteworthy that almost all the food taken is moving; probably they only take food casually as it moves in their line of vision. From April to July *T. inermis* is all important. Robertson (1932), writing of his voyage to Bear I. in July, 1930, says: "On occasions the cod were packed with this 'krill' and vomited it in great quantity all over the deck. They seemed to feed on nothing else." In August, 1936, *T. inermis* was dominant in our samples which were taken from the south-east of the island, but Brotsky, while showing it as important on the southern slope, gives *Euthemisto libellula* as the predominant food on the eastern slope; the patchy nature of euphausiacean distribution, however, is well known. Capelins are a prominent feature of our August samples. In September we found *Parathemisto* and *Euthemisto* together with herring and polychaetes to be most prominent. *Thysanöessa* for the rest of the year forms but an insignificant part of the diet. October shows a mixture, with polychaetes and amphipods again very important in



our samples and ophiuroids coming third. Ophiuroids, particularly *Ophiopholis aculeata* and *Ophiura* spp., continue to be important for the rest of the year. The few samples taken in October from the Spitzbergen Bank showed herring predominating. In November at Bear I. we found young herring (3-4 inches) to lead over a general mixture with ophiuroids second, but Brotsky in 1930 found for November "the food consists entirely of herring." At Spitzbergen in November we found ophiuroids greatly predominating. In December both Brotsky's and our records show a mixed diet; in our samples ophiuroids predominate in 1936, but in 1937 young herring take a marked lead.

TABLE II.—*A List of the more important Animals consumed by the Cod off Bear Island in Different Months throughout the year, as recorded by Brotsky (B) and Robertson (R) in 1930, and by Brown and Cheng in the present investigation (1936-38). Those in a heavy type are the species which appear to be of greater importance in the different months.*

|        | January.                        | February.          | March.              | April.             | May.               | June.              |
|--------|---------------------------------|--------------------|---------------------|--------------------|--------------------|--------------------|
| 1930 . | <b>Thysanöessa</b> <sup>1</sup> | ..                 | ..                  | <b>Thysanöessa</b> | ..                 | <b>Thysanöessa</b> |
| (B)    | Parathemisto <sup>1</sup>       |                    |                     | Codling            |                    | Hippolyte          |
|        | Euthemisto <sup>1</sup>         |                    |                     | Gadoids            |                    | Hyas               |
|        | Pandalus                        |                    |                     | Triglops           |                    | Eupagurus          |
|        | Ophiopholis                     |                    |                     |                    |                    | Herring            |
|        | Triglops                        |                    |                     |                    |                    |                    |
| 1937 . | ..                              | ..                 | ..                  | ..                 | <b>Thysanöessa</b> | ..                 |
|        |                                 |                    |                     |                    | Parathemisto       |                    |
|        |                                 |                    |                     |                    | Euthemisto         |                    |
| 1938 . | <b>Thysanöessa</b>              | <b>Pandalus</b>    | <b>Parathemisto</b> | <b>Thysanöessa</b> | <b>Thysanöessa</b> | ..                 |
|        | Ophiopholis                     | Thysanöessa        | Thysanöessa         | Herring            |                    |                    |
|        | Ophiura                         |                    |                     |                    |                    |                    |
|        | Herring                         |                    |                     |                    |                    |                    |
|        | July.                           | August.            | September.          | October.           | November.          | December.          |
| 1930 . | <b>Thysanöessa</b>              | <b>Euthemisto</b>  | ..                  | Mesidothea         | <b>Herring</b>     | Pandalus           |
| (B)    | Codling                         | Thysanöessa        |                     | Sabinea            |                    | Phascolosoma       |
|        |                                 | Anonyx             |                     | Herring            |                    | Herring            |
|        |                                 | Codling            |                     | Boreogadus         |                    | Gadoids            |
|        |                                 | Triglops           |                     | Triglops           |                    | Triglops           |
| (R)    | <b>Thysanöessa</b>              | ..                 | ..                  | ..                 | ..                 | ..                 |
| 1936 . | ..                              | <b>Thysanöessa</b> | ..                  | ..                 | ..                 | <b>Ophiopholis</b> |
|        |                                 | Parathemisto       |                     |                    |                    | <b>Ophiura</b>     |
|        |                                 | Euthemisto         |                     |                    |                    | Pandalus           |
|        |                                 | Capelin            |                     |                    |                    |                    |
| 1937 . | ..                              | ..                 | <b>Parathemisto</b> | <b>Polychaetes</b> | <b>Herring</b>     | <b>Herring</b>     |
|        |                                 |                    | <b>Euthemisto</b>   | Parathemisto       | Ophiopholis        | Ophiopholis        |
|        |                                 |                    | Polychaetes         | Euthemisto         | Ophiura            | Ophiura            |
|        |                                 |                    | Herring             | Ophiopholis        | Parathemisto       | Pandalus           |
|        |                                 |                    |                     | Ophiura            | Euthemisto         |                    |
|        |                                 |                    |                     | Herring            |                    |                    |
|        |                                 |                    |                     | Codling            |                    |                    |

<sup>1</sup> Brotsky used the old name Rhoda for Thysanöessa, and Themisto for Parathemisto and Euthemisto.

The small fish, *Triglops pingelii* Reinhardt, while present in our samples (see Appendix II), did not appear to play so important a part as in 1930, for Brotsky mentions it for that year in January, April, August, October and December.

While Text-fig. 5 and Table II show the general trend of feeding throughout the year, there may be a very considerable difference in the food taken in different situations at any one period. In the eleven-day period Oct. 31 to Nov. 10, 1937, we have a number of samples from widely separated regions round the island. Although the number of samples is very small, they indicate clearly the big differences in the food taken by the cod in different parts of the area in the same period. This is shown graphically in Text-fig. 7, and is no doubt due to the patchy nature of the bottom fauna. Polychaetes predominate in the N.E., amphipods to the E.N.E., whilst these vie with codling to the N.W.; ophiuroids predominate at E.×S., E.S.E. and S.×E., herring at E.×N., W.×S. and W., and codling at S.E. and S. The actual quantities in themselves are of little significance because the numbers of samples (shown against each histogram) are so small. Against the position of each sample on the map we show the quantity of cod (in baskets) taken in the hauls; they suggest that the cod at this season is not congregating in one region where a particular favourite food is to be had.

In the same way we may compare in Text-fig. 5 the feeding of the cod on the Spitzbergen Bank with that at Bear I. for late October and November, 1937. These differences have already been commented on.

In spite of the differences shown in the feeding of the cod in different areas during the same period, there can be no doubt about the great importance of the pelagic Crustacea, particularly the euphausiacean, *Thysanöessa inermis*, as shown in Text-fig. 5 and Table II, during the spring and summer months. It is only in the winter when the pelagic Crustacea are scarce that the cod turn to a more mixed diet of benthic animals or of herring (in October and November). Brotsky (1931) says: "It should be noted that the cod does not feed on fish and on the pelagic crustacea at the same time, but that one is a substitute for the other." While this may usually be so, it is not always true; in our samples euphausiaceans and pelagic amphipods were taken with capelins in August, 1936, and with herring in September, 1937 (see Text-fig. 5). At times the lower half of a stomach might be packed with polychaetes and the upper half with euphausiaceans.

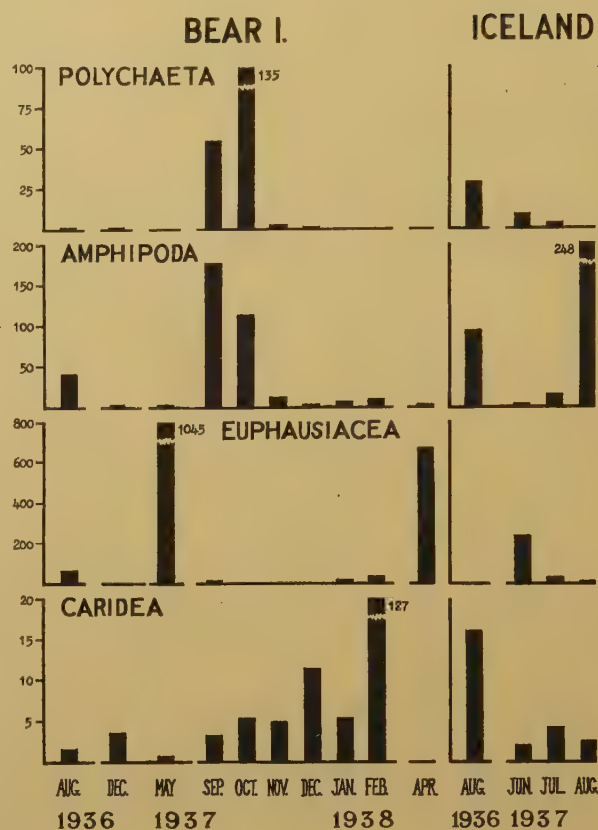
Owing to the lack of samples in June and July, it is not possible from our data to give a complete picture of the seasonal variation in the intensity of feeding throughout the year. From Table I it will be seen that the proportion of stomachs containing food is, on the whole, highest in August and September, after which a considerable reduction takes place. Brotsky's curve of percentage of empty stomachs shows that feeding is highest from August to October, after which there is a marked decline. The two sets of data clearly show that the cod off Bear I. are feeding most voraciously in the late summer and early autumn.

*Murman Coast and Andanes.*

In the short period December 29th, 1936, to January 5th, 1937, we have 90 stomachs collected from the Murman coast and in the following year, 29th Jan.-23rd Feb., 1938, we have 51 stomachs from two voyages fishing off Andanes (Andö I.) at the north end of the Lofoten Islands. For positions see Text-figs. 2 and 3.

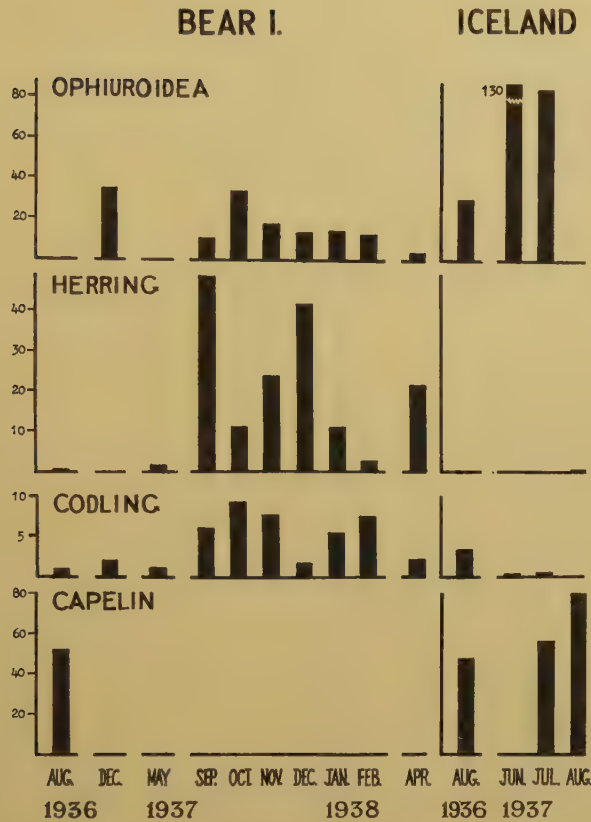
The food of the cod off the Murman Coast at this season was composed largely of capelin, Ophiuroidea and Caridea, as shown in Text-figs. 8 and 10. The order of numerical importance of various groups of more prominent food animals is as follows: Fish (52%), Crustacea (22%), Echinodermata (20%) and Actiniaria (3%). Of various species of fish, the most important is capelin, the next *Gasterosteus*, the third codling and the fourth herring. Noteworthy is the scarcity of Polychaeta and Euphausiacea in the diet. As compared with the food of the cod off Bear I. during the same period, the chief difference lies in the occurrence of herring and capelin off the Murman coast (Text-fig. 8).

The cod off Andanes were feeding almost entirely upon fish, especially sand-eels, which constitute no less than 75% of total fish; *Gadus poutassou* comes next in importance. We have not found the latter species elsewhere, but Brotsky mentions it being taken at Bear I. during January. The cod in this region had a very poor appetite at the time of collection, as more than half of the stomachs taken were found to be empty (69%). As stated in regard to the winter feeding at Bear I., it is likely that the cod are really not making any selection of food here, but are casually taking whatever is moving in their line of vision. They are collecting here for spawning rather than feeding.



TEXT-FIG. 6.—Histograms showing the same data as given in Text-fig. 5 for Bear Island, but arranged together with similar data for Iceland, to show group by group the seasonal fluctuations in the numbers of the more important food organisms being taken by the cod. The data for March and May, 1938, from Bear Island are here omitted as they are based on so small a number of stomachs (see Appendix III, Table I).





TEXT-FIG. 6 (cont.).

The material from Iceland is much more limited in extent, being confined to the months of June to August (one voyage in August, 1936, and seven voyages between June 1st and August 10th, 1937), and being collected almost entirely from off the north and east of the island.<sup>1</sup> Text-fig. 4 shows the positions from which the samples were taken. Altogether 257 stomachs were examined; of these 231 contained food.

As far as we are aware, the only other special study on the food of the cod at Iceland, apart from isolated observations, is that of Meschkat (1936), which, although based on larger numbers of stomachs (1245), is even more limited in space and time than ours. His observations are confined to the south of Iceland and for a short period, February 28th to March 23rd, 1935.

More work at Iceland is clearly

needed, but the two sets of data together provide some contributions towards a more general picture.

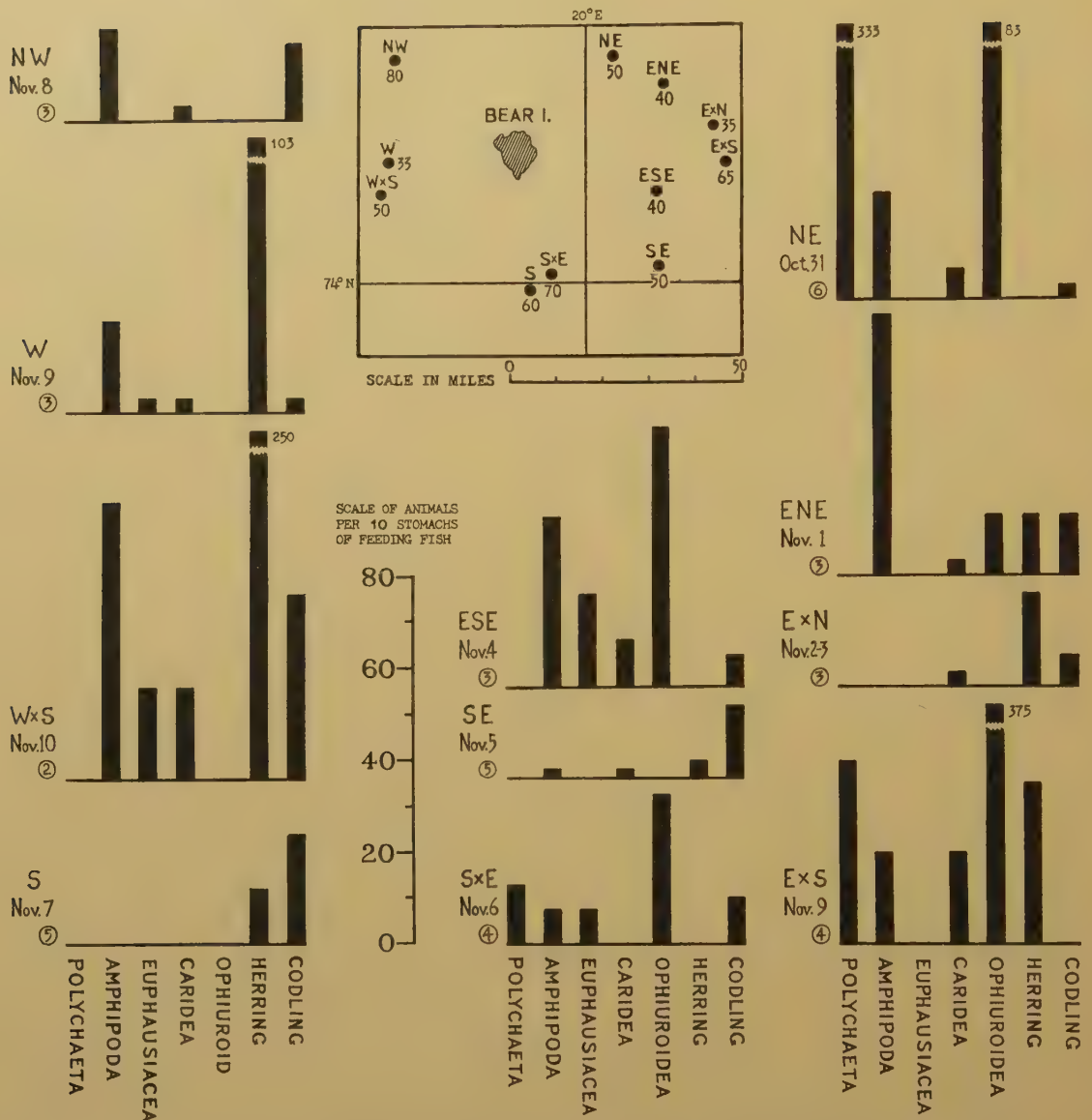
The number of different species identified in our Icelandic samples of cod stomachs are as follows:

|               |   |   |   |   |    |
|---------------|---|---|---|---|----|
| Actiniaria    | . | . | . | . | 0  |
| Polychaeta    | . | . | . | . | 11 |
| Crustacea     | . | . | . | . | 25 |
| Pycnogonida   | . | . | . | . | 0  |
| Mollusca      | . | . | . | . | 13 |
| Gephyrea      | . | . | . | . | 4  |
| Echinodermata | . | . | . | . | 6  |
| Pisces        | . | . | . | . | 6  |

A full list of the different species with details of their occurrence is given in Appendix II.

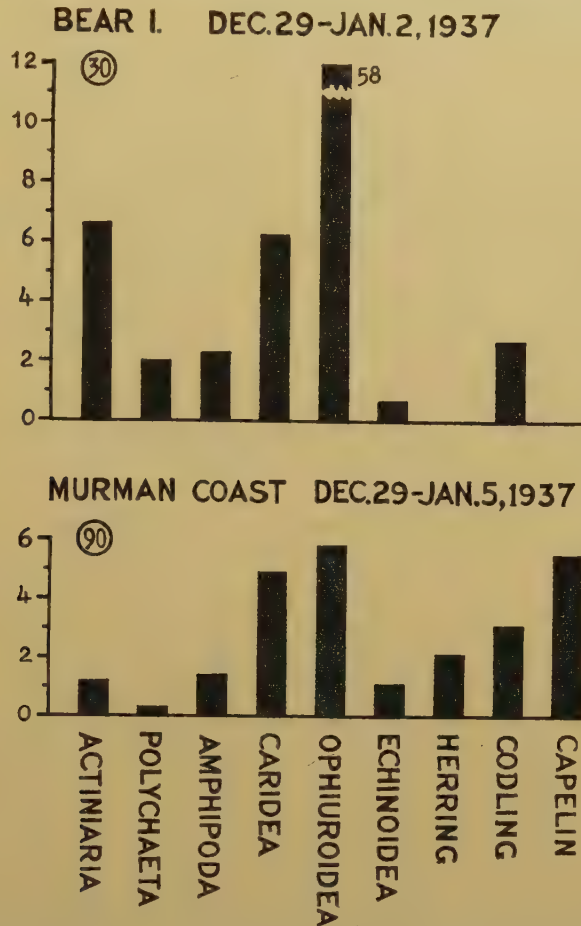
Text-fig. 9 shows a comparison of the food taken in the different regions in

<sup>1</sup> The data from voyage A (1933) are not included in the general discussion; see p. 37.



TEXT-FIG. 7.—Histograms showing the relative numbers of the more important food animals of the cod taken at various positions round Bear Island during the period Oct. 31st–Nov. 10th, 1937; expressed as average numbers per 10 stomachs of feeding fish. The numbers of stomachs containing food are shown in circles. The catches of cod (in baskets) are shown in the map against the positions (see Appendix III, Table II).

our investigation. The following are the main points of interest: In August, 1936, the only fish taken in large numbers were sand-eels in region B1 and capelin in regions B2 and B3. Polychaetes, carids and ophiuroids were important food animals in region B2, and amphipods were common in region B3. In June, 1937, the great abundance of euphausiaceans, mostly *Thysanoessa inermis*, taken in



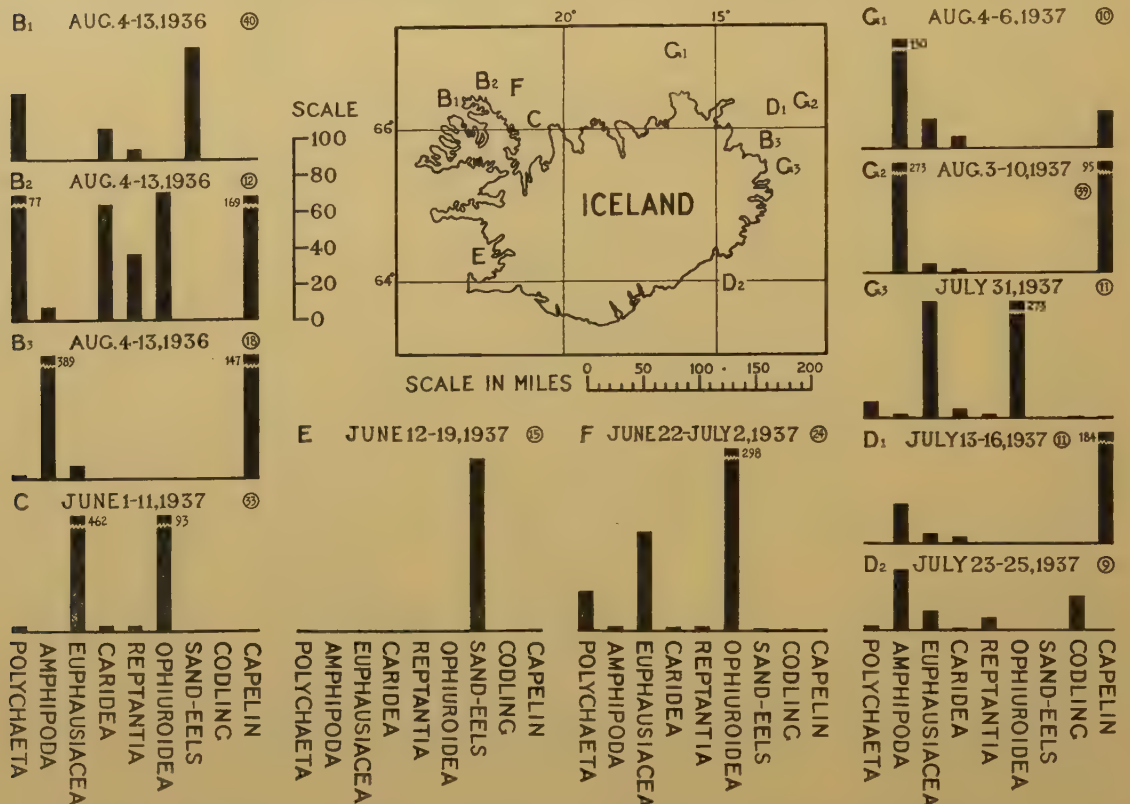
TEXT-FIG. 8.—Histograms showing a comparison of the stomach contents of the cod taken off Bear Island and the Murman Coast during the same period, expressed as average numbers per 10 stomachs of feeding fish. The numbers of stomachs containing food are shown in circles (see Appendix III, Table III).

region C, and their absence in region E, is very striking; in the latter region the cod fed upon nothing else but sand-eels. The food in region F is not dissimilar from that in region C, except for the relative changes in proportions of Euphausiacea and Ophiuroidea in the former region. In July and August, 1937, the food taken in regions G1, G2 and D1 is more or less the same, pelagic amphipods (mostly *Parathemisto obliqua*) and capelin predominating, the capelin being eaten



in much larger numbers in D1 and G2. It is noteworthy that in region G3, lying so near to regions D1 and G2, capelin are absent and amphipods are taken in much smaller numbers, euphausiaceans and ophiuroids predominating. The food taken in region D2 is smaller in quantity than in other regions, being dominated by amphipods.

Meschkat (1936) finds the food of the cod (for his limited period) consisting



TEXT-FIG. 9.—Histograms showing the relative numbers of the more important food organisms of the cod at different positions around Iceland during the periods Aug. 4th–13th, 1936, and June 1st–Aug. 10th, 1937, expressed as average numbers per 10 stomachs of feeding fish. The numbers of stomachs containing food are shown in circles (see Appendix III, Table IV).

largely of Crustacea (36.6%) and fish (32.1%). Of the former group, the most dominant species is *Crangon Allmanni* which is, however, unimportant in the present investigation, being recorded only once in voyage B (see Appendix II). As compared with our results, another difference lies in the relative importance of Echinodermata and Mollusca. The former group is of greater importance in the present investigation than in his, whilst the reverse holds true of the latter group. It should be emphasized, however, that the two sets of data are not strictly comparable, as the place and season of collection are different.

*The Principal Food Organisms in these and other Areas Compared.*

(1) Ctenophora : Owing to the advanced state of digestion, no identification can possibly be made of the jelly-like material in the samples obtained from Bear I. (voyage C) and the Murman Coast. One species of Ctenophore, *i.e.* Berøe sp., is, however, recorded by one of the authors (W.W.B.) as occurring in the stomachs taken off Bear I. (voyage C). Jensen and Hansen (1931) state that "Ctenophores, Berøe sp. and Bolina sp., are often consumed in large quantities" in the Greenland area. Poulsen (1931) finds Pleurobrachia in the stomachs of large cod (50 cm.) taken from Danish waters.

(2) Actiniaria are of frequent occurrence in the stomachs obtained from Bear I. and the Murman Coast. They are known to be eaten by the cod off Greenland (Jensen and Hansen, 1931) and in Danish waters (Blegvad, 1916). In the former area the cod taken from deep waters off Nuk are found to feed almost entirely upon these animals (see Appendix I).

(3) *Aphrodite aculeata* L. is recorded as an important food animal in Icelandic waters (Meschkat, 1936), North Sea (Brook, 1885; Todd, 1905, 1907; Graham, 1923; Hertling, 1938) and Danish waters (Blegvad, 1916; Poulsen, 1931). According to Brook (1885), "Aphrodite forms an important part of the food in the spring and summer in districts where this form is plentiful."

(4) *Parathemisto oblivia* is of great importance in the present investigation, occurring most abundantly off Langenes, Iceland, during August, 1936 and 1937. Its occurrence in the cod stomachs has been recorded for the Bear I. by Brotsky (1931) and Robertson (1932).

(5) *Euthemisto likellula* is not infrequently met with in the stomachs obtained from Iceland and Bear I. Brotsky (1931) records it as being the principal food animal off Bear I. in August, 1930.

(6) *Meganyctiphanes norvegica*<sup>1</sup> occurs only in the stomachs taken off Iceland. It is known to be eaten by the cod in Icelandic waters (Meschkat, 1936; Stephensen, 1938), and Barents Sea (Brotsky, 1931).

(7) *Thysanoessa inermis*<sup>1</sup> is, on the whole, more important than *Meganyctiphanes* in the present investigation, particularly off Bear I., where it forms the principal food of the cod during the summer months, as shown too by Brotsky (1931) and Robertson (1932). Its occurrence in the cod stomachs has also been recorded for Finmark by Hansen (1908) and for Iceland by Saemundsson (1937).

(8) *Pandalus borealis* is the most important species of Caridea found in the present investigation, being encountered in many samples obtained from Iceland, Bear I. and the Murman Coast. According to Saemundsson (1937), it plays a very important part in the food of the cod in Icelandic waters. It is known to be

<sup>1</sup> Einarsson (1945), in his important account of the Euphausiacea of the North Atlantic, draws attention to the leading part played by *Th. inermis* as food in the sub-arctic area, and to that by *M. norvegica* in boreal waters. He also refers to the detailed observations on the food of Cod in the southern Barents Sea by Zatsepin and Borova (1939) which we have been unable to see. Apparently they found euphausiaceans to be "second in importance as food items in this area" (Einarsson 1945, p. 162).

consumed by the cod in the Greenland area (Jensen and Hansen, 1931), Barents Sea (Brotsky, 1931), and Danish waters (Poulsen, 1931).

(9) *Crangon Allmanni* is unimportant in the present investigation, occurring only in one sample obtained from Iceland (voyage B). Meschkat (1936) records it, however, as being the most dominant food animal off the south of Iceland. It is also found in the cod stomachs taken from the North Sea (Brook, 1885 ; Todd, 1905 ; Hertling, 1938) and Danish waters (Poulsen, 1931).

(10) *Eupagurus* spp.: *E. pubescens* is of frequent occurrence in the samples procured from Iceland and Bear I. *E. Bernhardus* (L.) is eaten by the cod in the North Sea (Brook, 1885 ; Todd, 1905, 1907 ; Graham, 1923 ; Hertling, 1938) and Danish waters (Poulsen, 1931). According to Todd (1905), the latter species is of great importance in the North Sea.

(11) *Hyas coarctatus* is fairly common in all our areas ; it is consumed by the cod off Newfoundland (Thompson, 1943), Greenland (Jensen and Hansen, 1931), Iceland (Meschkat, 1936 ; Saemundsson, 1937), and in the North Sea (Brook, 1885 ; Todd, 1905, 1907 ; Graham, 1923 ; Hertling, 1938).

(12) *Portunus* spp. are absent in our samples, but are recorded as important food animals in Icelandic waters (Meschkat, 1936), Irish Sea (Johnstone, Scott and Smith, 1923), North Sea (Brook, 1885 ; Todd, 1905 ; Graham, 1923), and Danish waters (Poulsen, 1931).

(13) *Gonatus fabricii* is present in the samples obtained from Bear I. and the Murman Coast. It is of interest to note that in the Greenland area the young of this species constitute the principal food of the cod in late summer, when they appear in large shoals (Jensen and Hansen, 1931).

(14) *Ophiopholis aculeata* is abundant as food in the present investigation, occurring frequently in the samples taken from Iceland during the summer months of 1936 and 1937. The cod in the Barents Sea (Brotsky, 1931), North Sea (Brook, 1885) and Danish waters (Blegvad, 1916) are found to feed eagerly upon this species.

(15) *Clupea harengus* is also very important in our samples, forming the principal food of the cod off Bear I. in November and December, as observed too by Brotsky (1931). It is recorded as the favourite food of the cod in the Newfoundland area (Thompson, 1943), Icelandic waters (Meschkat, 1936), North Sea (Brook, 1885 ; Todd, 1907 ; Graham, 1923 ; Hertling, 1938), and Danish waters (Blegvad, 1916 ; Poulsen, 1931).

(16) *Mallotus villosus* is no less important than herring in the present investigation, contributing largely to the food of the cod off Iceland in the summers of 1936 and 1937. It is recorded as a dominant food organism off Newfoundland (Thompson, 1943), Greenland (Jensen and Hansen, 1931), Iceland (Meschkat, 1936), Finmark (Iversen, 1924), and in the Barents Sea (Hjort, 1914 ; Iversen, 1924 ; Brotsky, 1931). Hjort (1914) states: "When the enormous shoals of capelin leave their northern quarters in winter and move towards the Finmark and Murman Coasts, they draw after them the shoals of cod, encountered on the way,



the latter pursuing and greedily devouring them. I have found between 20 and 30 of these fish in the stomach of a single cod."

(17) *Gadus callarias* (young) is common in our samples, and is also taken by the cod in the Barents Sea (Brotsky, 1931; Robertson, 1932), North Sea (Graham, 1923), and Danish waters (Blegvad, 1916; Poulsen, 1931).

(18) *Ammodytes* spp. play a very important rôle in the food of the cod off Andanes and Iceland, especially in the Faxø Bay, where the cod taken on June 12th to 19th, 1937, appeared to feed on nothing else but sand-eels. They are also recorded as important food animals off Newfoundland (Thompson, 1943), Greenland (Jensen and Hansen, 1931), Iceland (Meschkat, 1936), and in the North Sea (Brook, 1885; Todd, 1907; Graham, 1923), Danish waters (Poulsen, 1931) and Baltic Sea (Hertling, 1928).

#### THE FOOD OF THE HADDOCK.

Our haddock food material is confined to 40 stomachs collected on a voyage to Iceland, off North Cape, Strauminaes and Adelvig, from August 4th to 13th, 1936, and 137 stomachs collected on a voyage to the Murman Coast from December 29th, 1936, to January 5th, 1937.

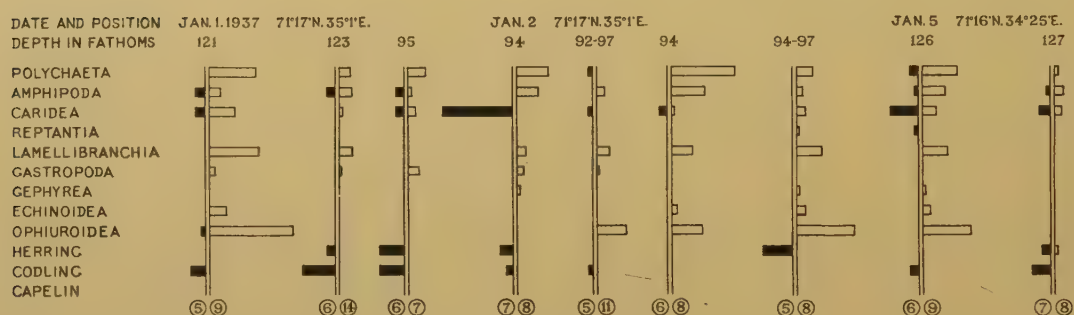
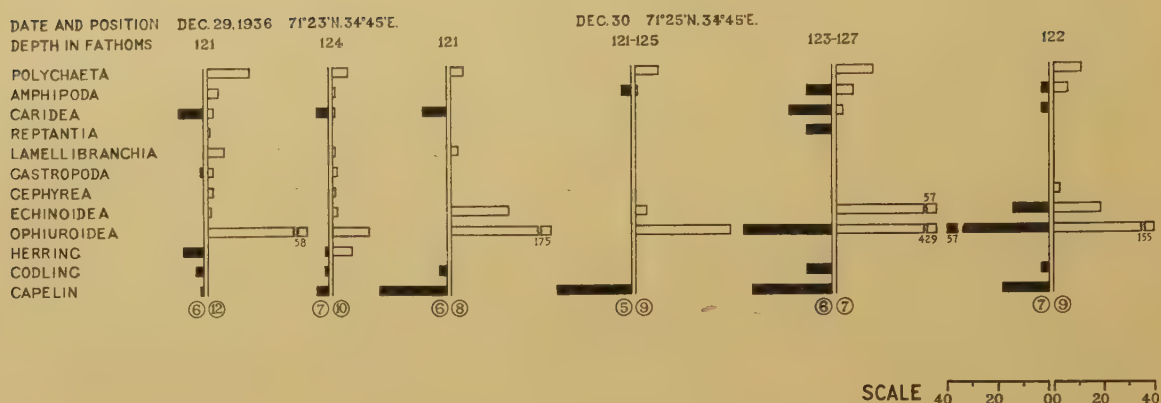
*Iceland.*—Polychaetes and ophiuroids are together overwhelmingly dominant in the samples from off the North Cape, but while polychaetes are just as abundant off Strauminaes and Adelvig, the ophiuroids are taken in only moderate numbers. The only fish taken were sand-eels, and they were absent from the North Cape samples, but second in importance off Strauminaes and less so off Adelvig. The relative importance of the different constituents of the food is clearly shown in the open histograms in Text-fig. 10. It is of interest to note the observation made by Thompson (1928) on the food of the haddock off Iceland, showing that the haddock off the north and north-west of the island feed mainly upon *Ophiopholis aculeata*, an ophiuroid, and *Terebellides Stromi*, a polychaete, whilst those off the south coast feed almost entirely upon sand-eels.

*Murman Coast.*—Here ophiuroids were most abundant in the food, with polychaetes and echinoids next in importance. Lamellibranchs were more important than in our Icelandic samples. The relative importance of the different organisms can again be seen in Text-Fig. 10.

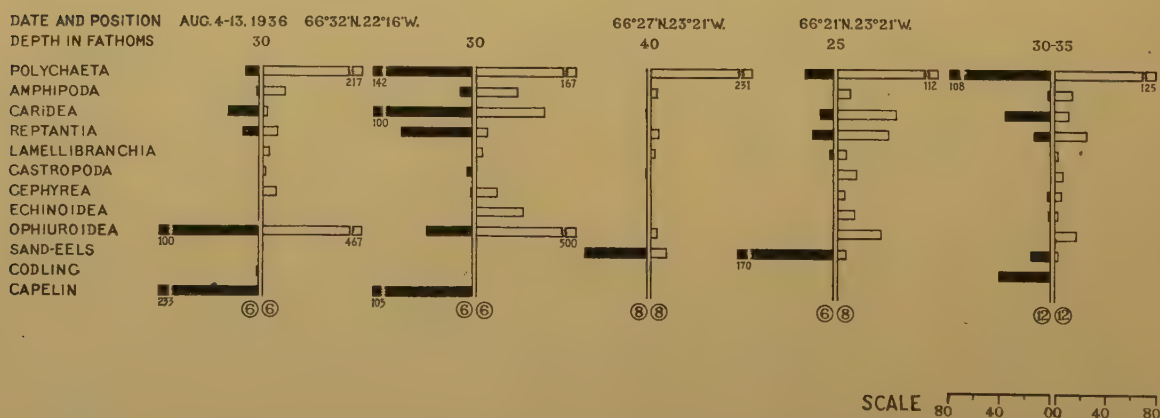
#### FEEDING OF COD AND HADDOCK COMPARED.

On the two voyages dealt with in the preceding section, one to Iceland and the other to the Murman Coast, stomachs of both cod and haddock were collected from the same trawl hauls. We have 20 of these cod and haddock samples—5 from Iceland and 15 from the Murman Coast. Since the fish were taken at the same time from the same ground, they provide a contribution towards a comparative study of the feeding of the two species; they give some answer to the important question: "To what extent do they compete for the same food?"

## MURMAN COAST



## ICELAND



TEXT-FIG. 10.—Showing a comparison between the food of the cod (black-in histograms) and that of the haddock (open histograms) taken in the same trawl hauls off the Murman Coast during the period Dec. 29th, 1936–Jan. 5th, 1937, and off Iceland during the period Aug. 4th–13th, 1936, expressed as average numbers per 10 stomachs of feeding fish. The numbers of stomachs containing food are shown in circles (see Appendix III, Tables V and VI). Note that the scale for Iceland is half that for the Murman Coast.

Since a single trawl haul covers a considerable distance—some four or five miles—and more cod than haddock may be taken from one part of the stretch and *vice versa* from another part, it might be thought that the variations found may be due to differences in the fauna on different parts of the ground rather than to any feeding selection being made by the two species. But when a good number of examples are considered, this possible explanation must be ruled out. In Text-fig. 10 the relative quantities of the different organisms eaten by cod and haddock taken from the same hauls are shown as blacked-in and open histograms opposite one another. It is seen that in both areas, Iceland and the Murman Coast, the haddock feed, on the whole, more heavily upon Polychaeta, Lamellibranchia, Gastropoda, Gephyrea, Echinoidea and Ophiuroidea than do the cod, and that the cod feed more heavily upon fish (herring, sand-eels, capelin and codling) than do the haddock.

In view of the possible objection raised at the beginning of the preceding paragraph, it may be well to set out the cod/haddock ratio, in regard to the groups of organisms just mentioned, as follows :

*Polychaeta.*

Iceland : 12/217, 142/167, 0/231, 23/113, 108/125.

Murman Coast : 0/17, 0/6, 0/5, 0/9, 0/14, 0/11, 0/19, 0/4, 0/7, 0/12, 2/0, 0/25, 0/6, 3/13, 0/1.

*Lamellibranchia.*

Iceland : 0/5, 0/5, 0/4, 0/4, 0/3.

Murman Coast : 0/7, 0/1, 0/3, 0/0, 0/0, 0/0, 0/20, 0/6, 0/0, 0/4, 0/5, 0/9, 0/10, 0/10, 0/0.

*Gastropoda.*

Iceland : 0/2, 5/0, 1/0, 3/15, 0/6.

Murman Coast : 2/3, 0/2, 0/0, 0/0, 0/0, 0/0, 0/2, 0/1, 0/4, 0/3, 0/1, 0/0, 0/0, 0/0, 0/0.

*Gephyrea.*

Iceland : 0/10, 2/17, 0/1, 0/6, 3/4.

Murman Coast : 0/3, 0/1, 0/0, 0/0, 0/0, 0/2, 0/0, 0/0, 0/0, 0/1, 0/0, 0/0, 0/1, 0/1, 0/0.

*Echinoidea.*

Iceland : 0/0, 0/38, 0/0, 0/14, 2/3.

Murman Coast : 0/2, 0/2, 0/24, 0/4, 0/57, 14/19, 0/7, 0/0, 0/0, 0/0, 0/0, 0/3, 0/4, 0/3, 0/0.

*Ophiuroidea.*

Iceland : 100/467, 38/500, 0/5, 0/35, 0/17.

— Murman Coast : 0/58, 0/13, 0/175, 0/38, 37/429, 57/156, 2/33, 0/0, 0/0, 0/0, 0/12, 0/13, 0/23, 0/19, 0/0.



In all the above it is clearly seen that haddock are feeding much more on these organisms than the cod, whereas for fish the reverse is true as follows :

*Herring.*

Iceland : Herring are absent in the samples.

Murman Coast : 8/0, 1/8, 0/0, 0/0, 0/0, 0/0, 0/0, 3/0, 10/0, 6/0, 0/0, 0/0, 12/0, 0/0, 3/1.

*Capelin.*

Iceland : 233/0, 105/0, 0/0, 0/0, 0/0.

Murman Coast : 2/0, 4/0, 27/0, 30/0, 33/0, 19/0, 0/0, 0/0, 0/0, 0/0, 0/0, 0/0, 0/0, 0/0, 0/0.

*Codling.*

Iceland : 2/0, 0/0, 0/0, 0/0, 42/0.

Murman Coast : 3/0, 1/0, 3/0, 0/0, 10/0, 3/0, 6/0, 13/0, 10/0, 3/0, 2/0, 0/0, 0/0, 3/0, 7/0.

*Sand-eels.*

Iceland : 0/0, 0/0, 50/13, 17/8, 17/3.

Murman Coast : Sand-eels are absent in the samples.

In regard to Crustacea there is, on the whole, little difference in the numbers taken by the two species. In an example from the North Sea, however, Todd (1905) observes that from the same trawl-haul cod were feeding almost entirely on Crustacea, and haddock upon Echinodermata and Mollusca. The variation in the cod/haddock ratios in respect to the three main groups of Crustacea represented in the present investigation is as follows :

*Amphipoda.*

Iceland : 2/17, 10/33, 0/5, 0/10, 2/13.

Murman Coast : 0/4, 0/1, 0/0, 4/1, 10/7, 3/6, 4/4, 3/6, 3/1, 0/9, 0/4, 0/14, 0/3, 2/9, 1/4.

*Caridea.*

Iceland : 25/3, 100/55, 1/0, 10/44, 37/11.

Murman Coast : 10/3, 4/1, 10/0, 0/0, 17/3, 3/0, 4/10, 0/1, 3/3, 29/0, 2/0, 3/1, 0/4, 12/6, 4/3.

*Reptantia.*

Iceland : 13/12, 58/8, 0/6, 17/40, 13/24.

Murman Coast : 0/1, 0/0, 0/0, 0/0, 10/0, 0/0, 2/0, 0/0, 0/0, 0/0, 0/0, 0/0, 0/1, 2/0, 0/0.

Table III summarizes the relative abundance of the main groups of food organisms in cod and haddock stomachs taken in the same trawl-hauls off Iceland and the Murman Coast.

TABLE III.—*Comparison of the Relative Numerical Proportions of Various Groups of Food Organisms of the Cod and Haddock taken off Iceland during the period August 4th to 13th, 1936, and off the Murman Coast during the period December 29th, 1936, to January 5th, 1937, expressed both as Average Numbers per 10 Stomachs of Feeding Fish and as Percentages of Total Food.*

|                     | Iceland. |     |          |     | Murman Coast. |     |          |     |
|---------------------|----------|-----|----------|-----|---------------|-----|----------|-----|
|                     | Cod.     |     | Haddock. |     | Cod.          |     | Haddock. |     |
|                     | Average. | %.  | Average. | %.  | Average.      | %.  | Average. | %.  |
| Actiniaria . . .    | 0.3      | 0.1 | 0        | 0   | 1.5           | 3   | 0.6      | 0.6 |
| Polychaeta . . .    | 57       | 22  | 164      | 40  | 0.4           | 0.9 | 10       | 10  |
| Crustacea . . .     | 57       | 22  | 57       | 14  | 10            | 22  | 8        | 8   |
| Pycnogonida . . .   | 0        | 0   | 0        | 0   | 0.3           | 0.7 | 1.4      | 1.4 |
| Mollusca . . .      | 2.1      | 0.8 | 9        | 2   | 0.4           | 0.9 | 6        | 6   |
| Gephyrea . . .      | 1.4      | 0.5 | 7        | 1.7 | 0             | 0   | 0.7      | 0.7 |
| Echinodermata . . . | 29       | 11  | 166      | 41  | 9             | 20  | 68       | 70  |
| Pisces . . .        | 114      | 44  | 5        | 1.2 | 23            | 52  | 2        | 2   |

#### SUMMARY.

(1) The present report is based mainly upon the examination of the stomachs of 1277 medium-sized cod, of which more than half (824) were collected from Bear Island during the years from 1936 to 1938 inclusive, and the rest from Spitzbergen Bank (55), Murman Coast (90), Andanes (51) and Iceland (257). In addition, 177 haddock stomachs were obtained, 40 from Iceland and 137 from the Murman Coast. The methods of collection and examination, together with sources of error involved, are briefly stated.

(2) The analysis of samples obtained from Bear I. and Spitzbergen Bank shows the importance of Polychaeta, Amphipoda (Hyperiidæ), Euphausiacea, Caridea, Ophiuroidea and Pisces (herring, capelin and codling) in the diet, and that the relative abundance of various food organisms is subject to seasonal variation. In general, pelagic Crustacea, especially the euphausiacean, *Thysanoessa inermis*, play the most important part in the food of the cod from February to August, and young herring from November to December, as shown in Table II. The results of the present investigation are considered with those of Brotsky (1931) and Robertson (1932), and the three sets of data together provide a record of the food and intensity of feeding throughout the year. A brief account is given of the food of the cod in other areas; noteworthy is the dominance of fish in the diet: capelin off the Murman Coast and sand-eels off Andanes and Iceland (particularly in the Faxø Bay). References are made to the occurrence of the principal food organisms in areas outside the present investigation.

(3) The food of the haddock off Iceland and the Murman Coast is recorded for very limited periods, and is found to be dominated by ophiuroids and polychaetes. The former group of food organisms is particularly important off the Murman Coast in mid-winter, when it constitutes no less than 70% of total food.

(4) A comparison is made of the stomach contents of the cod and haddock taken together in the same trawl. The haddock appears to feed, on the whole, more heavily upon Polychaeta, Lamellibranchia, Gastropoda, Gephyrea, Echinoidea and Ophiuroidea; the cod feeds more heavily upon fish (herring, capelin, codling and sand-eels). There is little preference between the two in regard to Crustacea in the seasons and places sampled.

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## APPENDIX I.

## REPORT BY PROFESSOR T. A. STEPHENSON ON THE ACTINIARIA.

Although some of the material is unrecognizable without a very detailed anatomical study, a good deal of it is reasonably well preserved considering that it represents stomach-contents. Apart from the more difficult specimens, there seem to be three common and well-known northern species represented. These are:

*Hormathia digitata* (O. F. Müll.). This is known from many localities off Labrador, Greenland, Iceland, Spitzbergen, Norway, Faeroes, Shetlands, in the North Sea, etc.

*Hormathia nodosa* (Fabr.). This is probably distinct from *H. digitata*, but some forms of the two species approach one another and it is possible that they hybridize. *H. nodosa* has a similar range to that of *H. digitata*, perhaps wider and rather more northern. It is not British as far as is known.

*Tealia felina* (Linnaeus), var. *lofotensis* (Dan.). *Tealia felina* has 4 varieties, of which three are British and one (v. *crassicornis*) arctic, not extending south to Britain. The var. *lofotensis* is a boreal form common off the northern parts of the British Isles as well as Norway, Kattegat, the Baltic, and probably Iceland.

It should be noted that my identification of the material as probably belonging to these species is *strictly provisional*. While I think the determination is likely to be correct, it could only be made certain by a very detailed anatomical and histological examination which I have not time to carry out. The difficulty is that there are species belonging to genera allied to *Hormathia* and *Tealia* which are superficially very similar to them, and even some *unrelated* species are not dissimilar. If the identifications given are correct, the families represented in the collection are *Hormathiidae* (*Hormathia*) and *Actiniidae* (*Tealia*).

## BEAR ISLAND.

VOYAGE B. Sample G1.—(a) Three anemones, all the same, and an object of similar texture, but uncertain nature. Almost certainly *Hormathiidae*, probably *Hormathia nodosa*.

(b) Eight specimens, probably all the same as those under (a).

Sample G2.—One probable *Hormathia nodosa*, and pieces which may be the same.

Sample G4.—Six specimens and two fragments. Very like those in voyage G, sample 8. Probably *Hormathia nodosa*.

*Sample G5.*—(a) Two specimens which seem to be typical *H. nodosa*, and one small one probably the same.

(b) Three specimens, very likely *H. digitata*.

VOYAGE *D*, *Sample 2.*—Indeterminable without close study.

*Sample 3.*—Indeterminable without close study.

VOYAGE *G*, *Sample 8.*—Two specimens, the larger of which looks like typical *H. nodosa*.

VOYAGE *Q*, *Sample 5.*—Two specimens. One seems to be a *Tealia* (or related genus) with circumscript sphincter and the right kind of retractors, and probably small verrucae. The other seems the same but is badly preserved.

VOYAGE *R*, *Sample 2.*—Indeterminable without close study.

#### SPITZBERGEN.

VOYAGE *F*, *Sample 2.*—Two probable *H. nodosa*.

VOYAGE *K*, *Sample 3.*—One probable *H. digitata* and a fragment.

*Sample 4.*—One probable *H. digitata*.

#### MURMAN COAST.

VOYAGE *M*, *Sample T75.*—(a) Four specimens, very likely all *H. digitata*.

(b) One large specimen in four pieces. Probably *H. nodosa*.

*Sample T76.*—Two anemones, one on a hermit. Probably both *H. digitata*.

*Sample T78.*—(a) One large specimen, probably *H. digitata*, one small one, probably the same.

(b) One very typical-looking *H. digitata* and one indeterminable specimen.

*Sample T81.*—Two specimens. One is very likely the same *Tealia*-like anemone as from Voyage *Q*, *Sample 5* (Bear Island). It has visible verrucae, and may well be *Tealia felina* var. *lofotensis*. The other specimen is too damaged to identify.

*Sample T82.*—(a) Indeterminable without close study.

(b) One probable *H. nodosa*. One smoother *Hormathia*-like specimen, with apparently six pairs of perfect mesenteries and a strong mesogloal sphincter—perhaps *Allantactis parasitica* or a smooth *H. digitata*?

#### ICELAND.

VOYAGE *F*, *Sample 7.*—Indeterminable without close study.

## APPENDIX II.

## A LIST OF THE OCCURRENCE OF FOOD ORGANISMS TAKEN BY COD AND HADDOCK AT ICELAND, BEAR ISLAND, SPITZBERGEN, MURMAN COAST AND OFF ANDANES.

The letters refer to the voyages, the dates of which are given in Table I in the text, and the positions shown in Text-figs. 1-4. The letters shown in *italics* refer to those where the organism was taken by the haddock. In the Bear Island and Spitzbergen column the asterisk indicates Spitzbergen.

| Species.                                                | Iceland.            | Bear Island and Spitzbergen (*). | Murman Coast (M) and Andanes (A). |
|---------------------------------------------------------|---------------------|----------------------------------|-----------------------------------|
| ACTINIARIA :                                            |                     |                                  |                                   |
| <i>Hormathia digitata</i> (O. F. Müller)                | ..                  | B, K*                            | M, <i>M</i>                       |
| <i>Hormathia nodosa</i> (Fabr.)                         | ..                  | B, F*, G                         | M                                 |
| <i>Tealia felina</i> (L.) var. <i>lofotensis</i> (Dan.) | ..                  | Q                                | M                                 |
| POLYCHAETA :                                            |                     |                                  |                                   |
| <i>Euphrosyne</i> sp.                                   | C                   | ..                               | ..                                |
| <i>Lepidonotus squamatus</i> (L.)                       | B, B                | ..                               | ..                                |
| <i>Phyllodoce groenlandica</i> Oersted                  | B, B, F, G          | B, C, D, E                       | <i>M</i>                          |
| <i>Phyllodoce</i> sp.                                   | A, B, C, D, G       | ..                               | M                                 |
| <i>Nereis pelagica</i> L.                               | B, B, D             | B                                | M                                 |
| <i>Nereis</i> sp.                                       | B, B                | ..                               | ..                                |
| <i>Nephtys</i> sp.                                      | B, B, F             | B, C, D, M                       | <i>M</i>                          |
| <i>Lumbrinereis fragilis</i> (O. F. Müller)             | B, G                | C, E, G                          | <i>M</i>                          |
| <i>Onuphis</i> sp.                                      | E                   | ..                               | ..                                |
| <i>Glycera capitata</i> Oersted                         | B, B, F             | C, G                             | <i>M</i>                          |
| <i>Glycera</i> sp.                                      | C                   | ..                               | ..                                |
| <i>Amphiteis</i> sp.                                    | ..                  | ..                               | <i>M</i>                          |
| <i>Pectinaria belgica</i> (Pallas)                      | B                   | ..                               | ..                                |
| <i>Cistenides granulata</i> (L.)                        | B, B, F             | ..                               | ..                                |
| <i>Ophelia limacina</i> (Rathke)                        | B                   | ..                               | ..                                |
| <i>Ammotrypane aulogaster</i> (Rathke)                  | ..                  | D, G                             | <i>M</i>                          |
| <i>Travisia forbesii</i> Johnston                       | B                   | ..                               | ..                                |
| <i>Brada villosa</i> (Rathke)                           | B, B                | G, Q                             | <i>M</i>                          |
| <i>Stylarioides plumosa</i> (O. F. Müller)              | B, B, D, G          | C, E                             | <i>M</i>                          |
| <i>Sabella fabricii</i> Kröyer                          | ..                  | ..                               | <i>M</i>                          |
| <i>Laonome Kröyeri</i> Malmgren                         | ..                  | ..                               | <i>M</i>                          |
| Unidentified species                                    | A, B, B, C, E, F, G | A, C, F, G, M, Q                 | <i>M</i>                          |
| ECHIURIDAE :                                            |                     |                                  |                                   |
| <i>Hamingia arctica</i> Dan. et Kor.                    | ..                  | G                                | ..                                |
| COPEPODA :                                              |                     |                                  |                                   |
| <i>Calanus finmarchicus</i> (Gunn.)                     | D                   | ..                               | ..                                |
| <i>Euchaeta norvegica</i> Boeck                         | D                   | Z                                | M                                 |
| <i>Caligus</i> sp.                                      | ..                  | A                                | ..                                |
| MYSIDACEA :                                             |                     |                                  |                                   |
| ? <i>Erythrops</i> sp.                                  | ..                  | ..                               | M, <i>M</i>                       |
| Unidentified sp.                                        | ..                  | T                                | ..                                |
| CUMACEA :                                               |                     |                                  |                                   |
| Unidentified sp.                                        | ..                  | ..                               | <i>M</i>                          |



| Species.                                            | Iceland.   | Bear Island and<br>Spitzbergen (*).          | Murman Coast (M)<br>and Andanes (A). |
|-----------------------------------------------------|------------|----------------------------------------------|--------------------------------------|
| ISOPODA :                                           |            |                                              |                                      |
| <i>Cirolana microphthalmus</i> Hoek. . . . .        | ..         | B                                            | ..                                   |
| <i>Aega psora</i> (L.) . . . . .                    | A, C, F    | P                                            | ..                                   |
| <i>Aega</i> sp. . . . .                             | C          | ..                                           | ..                                   |
| ? <i>Syscenus</i> sp. . . . .                       | ..         | ..                                           | A                                    |
| <i>Mesidotea Sabini</i> (Krøyer) . . . . .          | ..         | 1                                            | ..                                   |
| ? <i>Phryxus</i> sp. . . . .                        | ..         | ..                                           | M                                    |
| AMPHIPODA :                                         |            |                                              |                                      |
| <i>Hyperia galba</i> (Mont.) . . . . .              | ..         | C, D, G                                      | M, M                                 |
| <i>Parathemisto obliqua</i> (Krøyer) . . . . .      | B, D, G    | A, B, C, D, E, F, F*,<br>G, H, I, M, S, U, W | M                                    |
| <i>Euthemisto libellula</i> (Mandt.) . . . . .      | B          | C, D, E, I, K*                               | ..                                   |
| <i>Euthemisto bispinosa</i> (Boeck) . . . . .       | B          | C, D, E, F                                   | ..                                   |
| <i>Euthemisto</i> sp. . . . .                       | ..         | D                                            | ..                                   |
| <i>Hippomedon propinquus</i> G. O. Sars . . . . .   | ..         | P                                            | M, M                                 |
| <i>Hippomedon</i> sp. . . . .                       | A          | ..                                           | ..                                   |
| <i>Anonyx nugax</i> (Phipps) . . . . .              | ..         | B, T                                         | M                                    |
| <i>Anonyx Lilljeborgii</i> Boeck . . . . .          | B, B, D, F | B, C, D, E, F, G, H,<br>N, P.                | M, M                                 |
| <i>Anonyx</i> sp. . . . .                           | B          | C, G                                         | ..                                   |
| <i>Hoplonyx similis</i> G. O. Sars . . . . .        | ..         | M                                            | M                                    |
| <i>Hoplonyx cicada</i> (Fabr.) . . . . .            | ..         | B, C, F*, W                                  | ..                                   |
| <i>Menigrates obtusifrons</i> Boeck . . . . .       | ..         | O                                            | ..                                   |
| <i>Ampelisca Eschrichti</i> Krøyer . . . . .        | ..         | B, G, I, M                                   | M, M                                 |
| <i>Byblis affinis</i> G. O. Sars . . . . .          | ..         | ..                                           | M                                    |
| <i>Haploops tubicola</i> Lilljeb. . . . .           | B, B       | ..                                           | ..                                   |
| <i>Haploops robusta</i> G. O. Sars . . . . .        | ..         | B                                            | ..                                   |
| <i>Haploops</i> sp. . . . .                         | ..         | ..                                           | M                                    |
| <i>Paroedicerus lynceus</i> (M. Sars) . . . . .     | B          | ..                                           | M                                    |
| <i>Monoculodes</i> sp. . . . .                      | ..         | ..                                           | M                                    |
| <i>Aceros phyllonyx</i> (M. Sars) . . . . .         | ..         | O                                            | M                                    |
| <i>Aceros</i> sp. . . . .                           | ..         | ..                                           | M                                    |
| <i>Paramphithoë monocuspis</i> G. O. Sars . . . . . | B          | ..                                           | ..                                   |
| <i>Epimeria</i> sp. . . . .                         | ..         | ..                                           | M                                    |
| <i>Acanthozona cuspidata</i> (Lepechin) . . . . .   | ..         | ..                                           | M                                    |
| <i>Acanthonotosoma serratum</i> (Fabr.) . . . . .   | B          | ..                                           | ..                                   |
| <i>Syrrhoë crenulata</i> Goës. . . . .              | B          | G                                            | ..                                   |
| <i>Tiron acanthurus</i> Lilljeb. . . . .            | ..         | ..                                           | M                                    |
| <i>Pardalisca cuspidata</i> Krøyer . . . . .        | B, B, D, F | E, F, K*                                     | ..                                   |
| <i>Pardalisca abyssi</i> Boeck . . . . .            | B          | B                                            | ..                                   |
| <i>Pardalisca</i> sp. . . . .                       | ..         | G                                            | M                                    |
| <i>Eusirus cuspidatus</i> Krøyer . . . . .          | B          | B                                            | ..                                   |
| <i>Rhachotropis aculeata</i> (Lepechin) . . . . .   | ..         | B, C, G, M, U, Z                             | ..                                   |
| <i>Rhachotropis Helleri</i> Boeck . . . . .         | ..         | ..                                           | M                                    |
| <i>Halirages fulvocinctus</i> (M. Sars) . . . . .   | ..         | ..                                           | M                                    |
| <i>Paratylus Smitti</i> (Goës) . . . . .            | ..         | E                                            | ..                                   |
| <i>Melita dentata</i> (Krøyer) . . . . .            | B, F       | ..                                           | ..                                   |
| <i>Lilljeborgia fissicornis</i> (M. Sars) . . . . . | C          | ..                                           | M                                    |
| <i>Protomedea fasciata</i> Krøyer . . . . .         | B          | ..                                           | ..                                   |
| <i>Unciola leucopis</i> (Krøyer) . . . . .          | B, B       | ..                                           | ..                                   |
| <i>Caprella linearis</i> (L.) . . . . .             | ..         | ..                                           | M                                    |
| Unidentified species of Hyperiidæ . . . . .         | B, D, G    | C, D, E                                      | ..                                   |
| Unidentified species of Gammaridæ . . . . .         | A, B, B    | B, D, F, G, H, M                             | M, M                                 |

| Species.                                             | Iceland.            | Bear Island and<br>Spitzbergen (*).                                        | Murman Coast (M)<br>and Andanes (A). |
|------------------------------------------------------|---------------------|----------------------------------------------------------------------------|--------------------------------------|
| EUPHAUSIACEA :                                       |                     |                                                                            |                                      |
| <i>Meganyctiphanes norvegica</i> M. Sars . . .       | A, B, D, F, G . . . | .. . .                                                                     | ..                                   |
| <i>Thysanöessa inermis</i> (Krøyer) . . .            | C, D, F, G . . .    | A, C, D, E, F, F*,<br>G, H, I, M, O, P,<br>Q, S, T, U, W, X,<br>Y, Z . . . | A, M, <i>M</i>                       |
| CARIDEA :                                            |                     |                                                                            |                                      |
| <i>Pasiphae</i> (? <i>princeps</i> Smith) . . .      | .. . .              | W . . .                                                                    | ..                                   |
| <i>Hymenodora glacialis</i> (Buchholz) . . .         | .. . .              | W . . .                                                                    | ..                                   |
| <i>Pandalus Montagu</i> (Leach) . . .                | B, B, F . . .       | .. . .                                                                     | ..                                   |
| <i>Pandalus borealis</i> Krøyer . . .                | D, F . . .          | A, B, C, G, H, I, L,<br>M, P, Q, R, S, T, U . . .                          | M, <i>M</i>                          |
| <i>Pandalus</i> sp. . . .                            | B . . .             | B, M . . .                                                                 | ..                                   |
| <i>Spirontocaris spinus</i> (Sowerby) . . .          | B, B . . .          | C, E, G . . .                                                              | ..                                   |
| <i>Spirontocaris pusiola</i> (Krøyer) . . .          | B, B . . .          | .. . .                                                                     | ..                                   |
| <i>Spirontocaris</i> (? <i>polaris</i> (Sab.)) . . . | B . . .             | E, F, F*, G, M, R . . .                                                    | M                                    |
| <i>Spirontocaris</i> sp. . . .                       | B, B . . .          | B, G, S . . .                                                              | ..                                   |
| <i>Pontophilus spinosus</i> (Leach) . . .            | D . . .             | .. . .                                                                     | ..                                   |
| <i>Sabinea Sarsii</i> Smith . . .                    | .. . .              | D, F* . . .                                                                | M                                    |
| <i>Sabinea septemcarinata</i> (Sab.) . . .           | .. . .              | C, E, I . . .                                                              | <i>M</i>                             |
| <i>Sclerocrangon boreas</i> Phipps . . .             | .. . .              | I, K*, P, Q . . .                                                          | ..                                   |
| <i>Crangon Allmanni</i> Kinaham . . .                | B . . .             | .. . .                                                                     | ..                                   |
| Unidentified spp. . . .                              | B, C, G . . .       | C, E, F, M, S . . .                                                        | M                                    |
| ANOMURA :                                            |                     |                                                                            |                                      |
| <i>Galathea nexa</i> Embleton . . .                  | B, B . . .          | .. . .                                                                     | ..                                   |
| <i>Munida bamffica</i> (Pennant) . . .               | D . . .             | .. . .                                                                     | ..                                   |
| <i>Eupagurus pubescens</i> (Krøyer). . .             | A, B, B, C, D . . . | D, E, G, I, M, P, U,<br>W . . .                                            | ..                                   |
| <i>Eupagurus</i> sp. . . .                           | F . . .             | K*, M . . .                                                                | M                                    |
| Unidentified spp. of Paguridae . . .                 | A, B . . .          | D, F, F*, Z . . .                                                          | <i>M</i>                             |
| <i>Lithodes maia</i> L. . . .                        | .. . .              | K* . . .                                                                   | <i>M</i>                             |
| BRACHYURA :                                          |                     |                                                                            |                                      |
| <i>Hyas coarctatus</i> Leach . . .                   | A, B, C, D, F . . . | F*, G, K*, P, S . . .                                                      | M, A                                 |
| PYCNOGONIDA :                                        |                     |                                                                            |                                      |
| <i>Nymphon spinosum</i> Goods . . .                  | .. . .              | P . . .                                                                    | M, <i>M</i>                          |
| <i>Nymphon groosipes</i> Fabr. . . .                 | .. . .              | .. . .                                                                     | <i>M</i>                             |
| <i>Nymphon macronyx</i> Sars . . .                   | .. . .              | B . . .                                                                    | ..                                   |
| AMPHINEURA :                                         |                     |                                                                            |                                      |
| Chiton sp. . . .                                     | A, B . . .          | G, J* . . .                                                                | <i>M</i>                             |
| GASTROPODA :                                         |                     |                                                                            |                                      |
| <i>Margarita cinerea</i> Couth . . .                 | B, B . . .          | .. . .                                                                     | M                                    |
| <i>Gibbula tumida</i> Mont. . . .                    | B . . .             | .. . .                                                                     | ..                                   |
| <i>Littorina</i> sp. . . .                           | B . . .             | .. . .                                                                     | ..                                   |
| <i>Natica affinis</i> Gmel. . . .                    | B . . .             | .. . .                                                                     | ..                                   |
| <i>Natica</i> sp. . . .                              | .. . .              | .. . .                                                                     | <i>M</i>                             |
| <i>Velutina laevigata</i> Penn. . . .                | .. . .              | .. . .                                                                     | <i>M</i>                             |
| <i>Pilidium</i> sp. . . .                            | .. . .              | E . . .                                                                    | ..                                   |
| <i>Buccinum</i> sp. . . .                            | B . . .             | .. . .                                                                     | M                                    |
| <i>Chrysodomus turtoni</i> Bean . . .                | .. . .              | Q . . .                                                                    | ..                                   |
| <i>Neptunea despecta</i> L. . . .                    | B, B . . .          | .. . .                                                                     | ..                                   |
| <i>Trophon clavatus</i> Sars . . .                   | .. . .              | .. . .                                                                     | M                                    |

| Species.                                                 | Iceland.         | Bear Island and<br>Spitzbergen (*). | Murman Coast (M)<br>and Andanes (A). |
|----------------------------------------------------------|------------------|-------------------------------------|--------------------------------------|
| <b>GASTROPODA (cont.):</b>                               |                  |                                     |                                      |
| <i>Trophon clathratus</i> var. <i>gunneri</i> L. . . . . | B                | ..                                  | ..                                   |
| <i>Scaphander lignarius</i> L. . . . .                   | ..               | ..                                  | M                                    |
| <i>Cylichna alba</i> Brown . . . . .                     | ..               | P                                   | ..                                   |
| <i>Philine lima</i> Brown . . . . .                      | ..               | ..                                  | M                                    |
| <i>Clione limacina</i> Phipps . . . . .                  | ..               | ..                                  | M                                    |
| <i>Dendronotus robustus</i> Verrill . . . . .            | ..               | B                                   | ..                                   |
| Unidentified spp. . . . .                                | ..               | ..                                  | M                                    |
| <b>LAMELLIBRANCHIA:</b>                                  |                  |                                     |                                      |
| <i>Nucula</i> sp. . . . .                                | ..               | ..                                  | M                                    |
| <i>Leda minuta</i> Müll. . . . .                         | A                | ..                                  | M                                    |
| <i>Portlandia intermedia</i> M. Sars . . . . .           | ..               | P                                   | M                                    |
| <i>Portlandia lucida</i> Lovén . . . . .                 | A                | ..                                  | ..                                   |
| <i>Arca glacialis</i> Gray . . . . .                     | ..               | P                                   | M                                    |
| <i>Mytilus</i> sp. . . . .                               | B, D             | ..                                  | ..                                   |
| <i>Modiola modiolus</i> L. . . . .                       | F                | ..                                  | ..                                   |
| <i>Pecten groenlandicus</i> Sow. . . . .                 | ..               | H                                   | M                                    |
| <i>Pecten islandicus</i> Müll. . . . .                   | ..               | E, F                                | ..                                   |
| <i>Astarte crebricostata</i> Forb. . . . .               | ..               | ..                                  | M                                    |
| <i>Astarte</i> sp. . . . .                               | ..               | H                                   | ..                                   |
| <i>Tridonta borealis</i> Chem. . . . .                   | B                | T                                   | ..                                   |
| <i>Cardium elegantulum</i> Beck . . . . .                | ..               | ..                                  | M                                    |
| <i>Cardium fasciatum</i> Mont. . . . .                   | B                | ..                                  | ..                                   |
| <i>Cardium echinatum</i> L. . . . .                      | D                | ..                                  | ..                                   |
| Unidentified spp. . . . .                                | A, B             | G                                   | M                                    |
| <b>CEPHALOPODA :</b>                                     |                  |                                     |                                      |
| <i>Rossia glaucopsis</i> Lovén . . . . .                 | B                | B, C                                | M, M                                 |
| <i>Ommatostrephes sagittatus</i> Lamarck . . . . .       | A                | ..                                  | ..                                   |
| <i>Gonatus fabricii</i> (Lichtenstein). . . . .          | ..               | A, C, G, T                          | M                                    |
| Unidentified spp. . . . .                                | D                | B, D, J*, M, R                      | ..                                   |
| <b>BRACHIOPODA :</b>                                     |                  |                                     |                                      |
| Unidentified spp. . . . .                                | ..               | ..                                  | M                                    |
| <b>PRIAPULOIDEA :</b>                                    |                  |                                     |                                      |
| <i>Priapulus caudatus</i> Lamarck . . . . .              | B, G             | ..                                  | ..                                   |
| <i>Priapulus bicaudatus</i> Daniel . . . . .             | G                | C                                   | M                                    |
| <b>SIPUNCULOIDEA :</b>                                   |                  |                                     |                                      |
| <i>Phascolosoma margaritaceum</i> (Sars) . . . . .       | B, B, F          | F*, G, K*, O, Q                     | M                                    |
| <i>Phascolosoma eremita</i> (Sars) . . . . .             | B, B             | ..                                  | ..                                   |
| <i>Phascolion strombi</i> (Montagu) . . . . .            | ..               | ..                                  | M                                    |
| <i>Onchnesoma squamatum</i> (Kor. et Dan.) . . . . .     | ..               | D                                   | ..                                   |
| <b>ASTEROIDEA :</b>                                      |                  |                                     |                                      |
| <i>Ctenodiscus crispatus</i> (Retzius) . . . . .         | ..               | ..                                  | M                                    |
| <i>Lophaster furcifer</i> (Duben and Koren) . . . . .    | C                | ..                                  | ..                                   |
| Unidentified spp. . . . .                                | A                | E                                   | ..                                   |
| <b>OPHIUROIDEA.</b>                                      |                  |                                     |                                      |
| <i>Ophiacantha bidentata</i> (Retzius) . . . . .         | A, B, F, G       | B, G, P, R                          | M, M                                 |
| <i>Ophiopholis aculeata</i> (L.) . . . . .               | A, B, B, C, F, G | B, C, D, E, G, P, Q, U              | M, M                                 |



| Species.                                                            | Iceland.         | Bear Island and<br>Spitzbergen (*).                                 | Murman Coast (M)<br>and Andanes (A). |
|---------------------------------------------------------------------|------------------|---------------------------------------------------------------------|--------------------------------------|
| <b>OPHIUROIDEA (cont.):</b>                                         |                  |                                                                     |                                      |
| <i>Ophiura Sarsi</i> Lütken . . . . .                               | ..               | B, C, D, E, F, F*,<br>G, K*, M, P, R,<br>T, U, Y                    | M, M                                 |
| <i>Ophiura robusta</i> Ayres . . . . .                              | A, B, B, F, G    | E, F, G, K*, P, Q                                                   | M, M                                 |
| <i>Ophiura albida</i> Forbes . . . . .                              | ..               | E                                                                   | ..                                   |
| <i>Ophiura</i> spp. . . . .                                         | ..               | B                                                                   | M, M                                 |
| Unidentified spp. . . . .                                           | A, G             | A, B, C, D, E, G,<br>M, P, R, T                                     | M, M                                 |
| <b>ECHINOIDEA :</b>                                                 |                  |                                                                     |                                      |
| <i>Strongylocentrotus drobachiensis</i> (O. F.<br>Müller) . . . . . | B, B, C, F       | D, E, G, P, Q, Y                                                    | M, M                                 |
| <i>Echinocyamus pusillus</i> (O. F. Müller) . . . . .               | B, F             | ..                                                                  | ..                                   |
| Unidentified spp. . . . .                                           | ..               | B                                                                   | ..                                   |
| <b>HOLOTHUROIDEA :</b>                                              |                  |                                                                     |                                      |
| Unidentified spp. . . . .                                           | A, B, B, C, F, G | M                                                                   | M, M                                 |
| <b>PISCES :</b>                                                     |                  |                                                                     |                                      |
| <i>Raia</i> (? <i>radiata</i> Donovan) . . . . .                    | D                | ..                                                                  | ..                                   |
| <i>Chupea harengus</i> (L.) . . . . .                               | G                | A, C, D, E, F, F*,<br>G, H, I, J*, L, M,<br>N, O, Q, S, T, U, X     | M, M                                 |
| <i>Mallotus villosus</i> (O. F. Müller) . . . . .                   | B, D, G          | C, G                                                                | M                                    |
| <i>Myctophum</i> sp. . . . .                                        | ..               | W                                                                   | ..                                   |
| <i>Gadus callarias</i> L. . . . .                                   | B, D, F, G       | A, B, C, D, E, F, F*,<br>G, H, I, J*, K*, M,<br>O, Q, S, T, U, W, X | M, A                                 |
| <i>Gadus aeglefinus</i> (L.) . . . . .                              | F                | E, G, K*, M, O, Q,<br>S, T, U                                       | M, A                                 |
| <i>Gadus poutassou</i> Risso . . . . .                              | ..               | ..                                                                  | A                                    |
| <i>Gadus esmarki</i> (Nilsson) . . . . .                            | ..               | ..                                                                  | M, M                                 |
| <i>Gadus virens</i> (L.) . . . . .                                  | ..               | K*, M                                                               | ..                                   |
| <i>Ammodytes</i> spp. . . . .                                       | B, B, E, F       | ..                                                                  | A                                    |
| <i>Lumpenus</i> sp. . . . .                                         | C                | C, D, E, G, H, I,<br>M, P, S                                        | ..                                   |
| <i>Lycodes</i> sp. . . . .                                          | D                | E, X                                                                | M                                    |
| <i>Lycenchelys</i> sp. . . . .                                      | ..               | E                                                                   | ..                                   |
| <i>Anarrhichas lupus</i> (L.) . . . . .                             | C                | E                                                                   | ..                                   |
| <i>Anarrhichas latifrons</i> (Steenstrup) . . . . .                 | ..               | C                                                                   | ..                                   |
| <i>Anarrhichas minor</i> (Olafsen) . . . . .                        | ..               | Q                                                                   | ..                                   |
| <i>Anarrhichas</i> sp. . . . .                                      | B, C, F          | ..                                                                  | ..                                   |
| <i>Sebastes marinus</i> (L.) . . . . .                              | ..               | ..                                                                  | M                                    |
| <i>Cottus</i> (? <i>bubalis</i> Euphrasen) . . . . .                | ..               | C, I                                                                | M                                    |
| <i>Trigla</i> sp. . . . .                                           | A, D             | D, J*, M, N, P, Q,<br>T                                             | A                                    |
| <i>Triglops pingelii</i> Reinhardt . . . . .                        | ..               | G, I, K*, M, P, Q,<br>T                                             | A                                    |
| <i>Gasterosteus</i> sp. . . . .                                     | ..               | ..                                                                  | M                                    |
| <i>Drepanopsetta</i> sp. . . . .                                    | D                | C, E, F, G, I, M,<br>T, U                                           | M, M                                 |
| Fish ova . . . . .                                                  | ..               | B, M, S                                                             | ..                                   |



TABLE II.—*Data used in Text-fig. 7, showing a Comparison of the more important Food Organisms of the Cod at different positions around Bear Island during the period from Oct. 31 to Nov. 10, 1937; expressed as average numbers per 10 Stomachs of Feeding Fish.*

| Position . . .                          | NE   | ENE  | E×N  | E×S    | ESE  | SE   | S×E  | S    | W×S  | W    | NW   |
|-----------------------------------------|------|------|------|--------|------|------|------|------|------|------|------|
| Date . . .                              | Oct. | Nov. | Nov. | Nov.   | Nov. | Nov. | Nov. | Nov. | Nov. | Nov. | Nov. |
|                                         | 31   | 1    | 2-3  | 9      | 4    | 5    | 6    | 7    | 10   | 9    | 8    |
| Depth (in fms.) .                       | 40   | 50   | 55   | 95-100 | 85   | 85   | 75   | 80   | 105  | 95   | 110  |
| Number of stomachs .                    | 7    | 3    | 5    | 5      | 8    | 8    | 6    | 6    | 2    | 3    | 4    |
| Number of stomachs<br>containing food . | 6    | 3    | 3    | 4      | 3    | 5    | 4    | 5    | 2    | 3    | 3    |
| Catch of cod (in baskets)               | 50   | 40   | 35   | 65     | 40   | 50   | 70   | 60   | 50   | 33   | 80   |
| Polychaeta . . .                        | 333  | 0    | 0    | 40     | 0    | 0    | 12   | 0    | 0    | 0    | 0    |
| Amphipoda . . .                         | 23   | 57   | 0    | 20     | 37   | 2    | 7    | 0    | 60   | 20   | 20   |
| Euphausiacea . . .                      | 0    | 0    | 0    | 0      | 20   | 0    | 7    | 0    | 20   | 3    | 0    |
| Caridea . . .                           | 7    | 3    | 3    | 20     | 10   | 2    | 0    | 0    | 20   | 3    | 3    |
| Ophiuroidea . . .                       | 83   | 13   | 0    | 375    | 57   | 0    | 32   | 0    | 0    | 0    | 0    |
| Herring . . .                           | 0    | 13   | 20   | 35     | 0    | 4    | 0    | 12   | 250  | 103  | 0    |
| Codling . . .                           | 3    | 13   | 7    | 0      | 7    | 16   | 10   | 24   | 40   | 3    | 17   |

TABLE III.—*Data used in Text-fig. 8, showing a Comparison between the Food of the Cod off Bear Island and that off the Murman Coast during the same period; expressed as average numbers per 10 Stomachs of Feeding Fish.*

| Locality . . .                           | Murman Coast.        | Bear Island.         |
|------------------------------------------|----------------------|----------------------|
| Date . . .                               | Dec. 29-Jan. 5, 1937 | Dec. 29-Jan. 2, 1937 |
| Number of stomachs . . .                 | 90                   | 55                   |
| Number of stomachs containing food . . . | 90                   | 30                   |
| Actiniaria . . .                         | 1.2                  | 7                    |
| Polychaeta . . .                         | 0.3                  | 2                    |
| Amphipoda . . .                          | 1.4                  | 2.3                  |
| Euphausiacea . . .                       | 0.5                  | 0                    |
| Caridea . . .                            | 5                    | 6                    |
| Reptantia . . .                          | 0.5                  | 0.7                  |
| Ophiuroidea . . .                        | 6                    | 58                   |
| Echinoidea . . .                         | 1.1                  | 0.7                  |
| Herring . . .                            | 2.1                  | 0                    |
| Codling . . .                            | 3.1                  | 3                    |
| Capelin . . .                            | 5.5                  | 0                    |



TABLE IV.—*Data used in Text-fig. 9, showing the Relative Numbers of the more important Food Organisms of the Cod at various positions around Iceland during the periods Aug. 4-13, 1936, and June 1-Aug. 10, 1937 ; expressed as average numbers per 10 Stomachs of Feeding Fish.*

| Voyage                             | B1              | B2  | B3  | C               | D1               | D2               | E                | F                    | G1             | G2              | G3            |
|------------------------------------|-----------------|-----|-----|-----------------|------------------|------------------|------------------|----------------------|----------------|-----------------|---------------|
| Period                             | Aug. 4-13, 1936 | ..  | ..  | July 1-11, 1937 | July 13-16, 1937 | July 23-25, 1937 | June 12-19, 1937 | June 22-July 2, 1937 | Aug. 4-6, 1937 | Aug. 3-10, 1937 | July 31, 1937 |
| Total number of stomachs           | 40              | 12  | 18  | 41              | 14               | 13               | 19               | 31                   | 10             | 39              | 11            |
| Number of stomachs containing food | 40              | 12  | 18  | 33              | 11               | 9                | 15               | 24                   | 10             | 39              | 11            |
| Average catch of cod (in baskets)  | 17              | 4   | 30  | 47              | 31               | 8                | 59               | 39                   | 5              | 32              | 7             |
| Polychaeta                         | 37              | 77  | 2   | 3               | ..               | 2                | ..               | 22                   | ..             | 1               | 9             |
| Amphipoda                          | 1               | 7   | 389 | 1               | 21               | 33               | ..               | 2                    | 150            | 273             | 2             |
| Euphausiacea                       | ..              | ..  | 7   | 462             | 5                | 11               | ..               | 54                   | 16             | 5               | 64            |
| Caridea                            | 17              | 63  | ..  | 3               | 3                | 1                | ..               | 2                    | 6              | 2               | 5             |
| Reptantia                          | 6               | 36  | ..  | 3               | ..               | 7                | ..               | 3                    | ..             | ..              | 2             |
| Ophiuroidea                        | ..              | 69  | ..  | 93              | ..               | ..               | ..               | 298                  | ..             | 1               | 273           |
| Sand-eels                          | 62              | ..  | ..  | ..              | ..               | ..               | 95               | 1                    | ..             | ..              | ..            |
| Codling                            | ..              | 1   | ..  | ..              | ..               | 19               | ..               | 1                    | ..             | ..              | 1             |
| Capelin                            | ..              | 169 | 147 | ..              | 184              | ..               | ..               | ..                   | 20             | 95              | 1             |

TABLE VI.—*Data used in Text-fig. 10, showing a Comparison between the Food of the Cod and that of the Haddock taken in the same Trawl Hauls off the North Coast of Iceland in the period August 4-13, 1936 ; expressed as average numbers per 10 Stomachs of Feeding Fish.*

| Cod and haddock                    | C   | H   | C   | H   | C  | H   | C   | H   | C   | H   |
|------------------------------------|-----|-----|-----|-----|----|-----|-----|-----|-----|-----|
| Number of stomachs containing food | 6   | 6   | 6   | 6   | 8  | 8   | 6   | 8   | 12  | 12  |
| Polychaeta                         | 12  | 217 | 142 | 167 | 0  | 231 | 23  | 112 | 108 | 125 |
| Amphipoda                          | 2   | 17  | 10  | 33  | 0  | 5   | 0   | 10  | 2   | 13  |
| Caridea                            | 25  | 3   | 100 | 55  | 1  | 0   | 10  | 44  | 37  | 11  |
| Reptantia                          | 13  | 12  | 58  | 8   | 0  | 6   | 17  | 40  | 13  | 24  |
| Lamellibranchia                    | 0   | 5   | 0   | 5   | 0  | 4   | 0   | 4   | 0   | 2   |
| Gastropoda                         | 0   | 2   | 5   | 0   | 1  | 0   | 3   | 15  | 0   | 6   |
| Gephyrea                           | 0   | 10  | 2   | 17  | 0  | 1   | 0   | 6   | 3   | 4   |
| Echinoidea                         | 0   | 0   | 0   | 38  | 0  | 0   | 0   | 14  | 2   | 2   |
| Ophiuroidea                        | 100 | 467 | 38  | 500 | 0  | 5   | 0   | 35  | 0   | 17  |
| Sand-eels                          | 0   | 0   | 0   | 0   | 50 | 12  | 170 | 7   | 17  | 3   |
| Codling                            | 2   | 0   | 0   | 0   | 0  | 0   | 0   | 0   | 42  | 0   |
| Capelin                            | 233 | 0   | 105 | 0   | 0  | 0   | 0   | 0   | 0   | 0   |

TABLE V.—Data used in Text-fig. 10, showing a Comparison between the Food of the Cod and that of the Haddock taken in the same Trawl Hauls off the Murman Coast during the period from Dec. 29, 1936, to Jan. 5, 1937; expressed as average numbers per 10 Stomachs of Feeding Fish.

| Dec. 29.        |    |   |    | Dec. 30. |     |   |    | Jan. 1. |    |    |   | Jan. 2. |   |   |    | Jan. 5. |    |    |    |   |   |
|-----------------|----|---|----|----------|-----|---|----|---------|----|----|---|---------|---|---|----|---------|----|----|----|---|---|
| C               | H  | C | H  | C        | H   | C | H  | C       | H  | C  | H | C       | H | C | H  | C       | H  | C  | H  |   |   |
| 6               | 12 | 7 | 10 | 6        | 8   | 5 | 9  | 6       | 14 | 6  | 7 | 7       | 8 | 5 | 11 | 6       | 8  | 6  | 9  | 7 | 8 |
| 0               | 17 | 0 | 6  | 0        | 5   | 0 | 9  | 0       | 19 | 0  | 4 | 0       | 7 | 0 | 12 | 0       | 25 | 3  | 13 | 0 | 1 |
| 0               | 4  | 0 | 1  | 0        | 0   | 4 | 1  | 3       | 6  | 3  | 1 | 1       | 3 | 1 | 9  | 0       | 14 | 2  | 9  | 1 | 4 |
| 10              | 2  | 4 | 1  | 10       | 0   | 0 | 0  | 0       | 10 | 0  | 1 | 3       | 3 | 0 | 2  | 3       | 1  | 12 | 5  | 4 | 2 |
| 0               | 1  | 0 | 0  | 0        | 0   | 0 | 0  | 0       | 0  | 0  | 0 | 0       | 0 | 0 | 0  | 0       | 0  | 2  | 0  | 0 | 0 |
| 0               | 7  | 0 | 1  | 0        | 2   | 0 | 0  | 0       | 20 | 0  | 6 | 0       | 0 | 0 | 4  | 0       | 9  | 0  | 10 | 0 | 0 |
| 2               | 2  | 0 | 2  | 0        | 0   | 0 | 0  | 0       | 2  | 0  | 1 | 0       | 4 | 0 | 5  | 0       | 0  | 0  | 0  | 0 | 0 |
| 0               | 2  | 0 | 1  | 0        | 0   | 0 | 0  | 0       | 0  | 0  | 0 | 0       | 0 | 0 | 1  | 0       | 0  | 0  | 0  | 0 | 0 |
| 0               | 2  | 0 | 1  | 0        | 0   | 0 | 0  | 0       | 0  | 0  | 0 | 0       | 0 | 0 | 0  | 0       | 0  | 0  | 1  | 0 | 0 |
| 0               | 1  | 0 | 2  | 0        | 24  | 0 | 4  | 0       | 7  | 0  | 0 | 0       | 0 | 0 | 0  | 0       | 2  | 0  | 3  | 0 | 0 |
| 0               | 58 | 0 | 13 | 0        | 175 | 0 | 38 | 37      | 33 | 0  | 0 | 0       | 0 | 0 | 12 | 0       | 12 | 0  | 19 | 0 | 0 |
| 8               | 0  | 1 | 8  | 0        | 0   | 0 | 0  | 0       | 0  | 10 | 0 | 0       | 0 | 0 | 0  | 0       | 0  | 0  | 0  | 3 | 1 |
| 3               | 0  | 1 | 0  | 3        | 0   | 0 | 0  | 10      | 0  | 10 | 0 | 0       | 0 | 2 | 0  | 0       | 0  | 3  | 0  | 7 | 0 |
| 2               | 0  | 4 | 0  | 0        | 33  | 0 | 30 | 33      | 0  | 0  | 0 | 0       | 0 | 0 | 0  | 0       | 0  | 0  | 0  | 0 | 0 |
| Cod and haddock |    |   |    |          |     |   |    |         |    |    |   |         |   |   |    |         |    |    |    |   |   |
| Number of       |    |   |    |          |     |   |    |         |    |    |   |         |   |   |    |         |    |    |    |   |   |
| stomachs con-   |    |   |    |          |     |   |    |         |    |    |   |         |   |   |    |         |    |    |    |   |   |
| taining food    |    |   |    |          |     |   |    |         |    |    |   |         |   |   |    |         |    |    |    |   |   |
| Polychaeta      |    |   |    |          |     |   |    |         |    |    |   |         |   |   |    |         |    |    |    |   |   |
| Amphipoda       |    |   |    |          |     |   |    |         |    |    |   |         |   |   |    |         |    |    |    |   |   |
| Caridea         |    |   |    |          |     |   |    |         |    |    |   |         |   |   |    |         |    |    |    |   |   |
| Reptantia       |    |   |    |          |     |   |    |         |    |    |   |         |   |   |    |         |    |    |    |   |   |
| Lamellibranchia |    |   |    |          |     |   |    |         |    |    |   |         |   |   |    |         |    |    |    |   |   |
| Gastropoda      |    |   |    |          |     |   |    |         |    |    |   |         |   |   |    |         |    |    |    |   |   |
| Gephyrea        |    |   |    |          |     |   |    |         |    |    |   |         |   |   |    |         |    |    |    |   |   |
| Echinoidea      |    |   |    |          |     |   |    |         |    |    |   |         |   |   |    |         |    |    |    |   |   |
| Ophiuroidea     |    |   |    |          |     |   |    |         |    |    |   |         |   |   |    |         |    |    |    |   |   |
| Herring         |    |   |    |          |     |   |    |         |    |    |   |         |   |   |    |         |    |    |    |   |   |
| Codling         |    |   |    |          |     |   |    |         |    |    |   |         |   |   |    |         |    |    |    |   |   |
| Capelin         |    |   |    |          |     |   |    |         |    |    |   |         |   |   |    |         |    |    |    |   |   |





# THE IDENTIFICATION AND CLASSIFICATION OF LAMELLIBRANCH LARVAE

BY

C. B. REES, M.Sc.

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## INTRODUCTION.

THE primary aim of this paper is to enable planktologists, with neither the time nor the inclination to specialize in the group, to identify lamellibranch larvae weeks or months after collection. For this, a method based on the shell rather than on the soft parts is necessary. Though the species to be described are those obtained in the North Sea, it is hoped that the method of analysis and the classification presented will greatly ease the task of identification in other areas, particularly in those areas where the lamellibranch bottom fauna is well known and the list of species fairly limited. The classification of the larvae has a direct

bearing on the classification of the Lamellibranchiata, but this major question is not being pursued here.

Descriptions of larval species have been given by several workers, but the planktologist could, from these, identify with confidence only a very few species, far fewer than those described. This is partly because the characteristics described are unsuitable for identification after preservation of the larvae, and also because few groups of larvae of allied species have been described so that it has not been clear how, and by how much, larvae of allied species differ.

Of papers already published, that by Werner (1939) may receive mention since he made a critical review of the larval features suitable for identification. The paper by Jørgensen (1946) is of considerable value, not least because of the comprehensiveness of the references. It would be superfluous to list again the earlier papers, and a reference to Jørgensen in the descriptive part should be taken as embracing the previous literature on the group or species in hand. The small number of described species has prevented any real attempt to establish a natural classification of larvae, though Bernard (1898), with little information, attempted a classification over a small field.

When the investigation was begun it was provisionally postulated that a natural classification of the larvae is possible, and it has become abundantly clear that this is so. The classification of the adults by Thiele (1935), which is now widely accepted, has been used in this report, since it is desirable that the classification of the larvae should conform as far as possible to that of the adults. A few minor adjustments have been made which are suggested by the practical advantage to be gained in the identification of lamellibranch larvae. It is of interest, however, that some of them have support from the classification given by Haas (1926).

The faunal lists of the lamellibranchs of the North Sea are given by Haas (1926). Much of the argument that follows regarding the species of the larvae depends on the accuracy and completeness of these lists. The specific names given by Winckworth (1932) or, when absent in Winckworth, by Haas (1926) are used. Since in some cases the reader might find it difficult to relate a specific name given by Winckworth to the faunal list of Haas the necessary synonyms are given in an appendix on p. 101.

I wish to take this opportunity of expressing my gratitude to Dr. A. C. Stephen for his considerable and unstinted help in many ways, and to Dr. D. Quayle, now of the Department of Fisheries, Victoria, B.C., Canada, who kindly kept me informed of the progress of his investigation of lamellibranch larvae whilst in this country and advised me to use photomicrographs instead of the less satisfactory line drawings.

Professor C. M. Yonge has been kind enough to read the paper in manuscript, and I am very grateful to him for his comments and advice, particularly on the systematics.

## METHODS.

Lamellibranch larvae are relatively heavy and can readily be separated from the rest of the plankton by gentle rotation of the containing dish, the larvae collecting together in the centre.

For identification to be based on shell structure it is essential to preserve the larvae in an alkaline medium. Formalin is suitable, at least for a few months, if thoroughly buffered with borax.

In the initial identification it is necessary to see the hinge clearly by separating the two valves from each other and from the soft parts. This can be done in a few minutes by immersing the larvae in sodium hypochlorite solution, 8-10% NaOH through which chlorine has been bubbled. In such a solution the valves gape and eventually fall apart, but the process can be speeded up by inserting the edge of a needle between the valves and wedging them open. The valves should not, in this process, be allowed to slide off each other since in some larvae the teeth break off readily.

The method of illustration by line drawings has proved unsuitable, as may be seen when comparing the drawings by different authors of the same species. Sullivan (1948), who has published photomicrographs of some species, expresses the same opinion. Photographs have usually been taken of single valves with the inside downwards. It is considered essential that this standard view should be adopted since a vaulted valve lying with inside up (or a complete larva) may take up a variety of positions with consequent changes in the apparent outline of the shell, changes as considerable as the difference between allied species.<sup>1</sup> That bivalves, and not the outside of isolated valves, have usually been drawn in previous papers may partly account for the differences in appearance of a species as shown by different authors.

Glycerine jelly is a particularly suitable medium for the observation of the hinge since the valves can be placed in any desired position with the aid of a hot needle. The inside view (see key in Text-fig. 3) is most easily seen and is sufficient where the hinge has an obvious feature or when the teeth are strong rectangular blocks. In cases where the teeth are not pronounced, or when they have sloping sides, the dorsal view assists greatly in an appreciation of the structure of the hinge.

For the dorsal view it is best to tilt the valve slightly from the true vertical so as to reveal more of the hinge structure. The gaps for teeth are roofed over by the shell of the valve and this "roof" is usually sufficiently opaque to hide structures underneath it, particularly the gaps for the reception of teeth.

<sup>1</sup> Sullivan's (1948) figs. 3 and 4, Plate X, of *Venus mercenaria* show that this is no exaggeration. The difference in shape between these two views of the same species is greater than the difference in shape within many pairs of allied species.

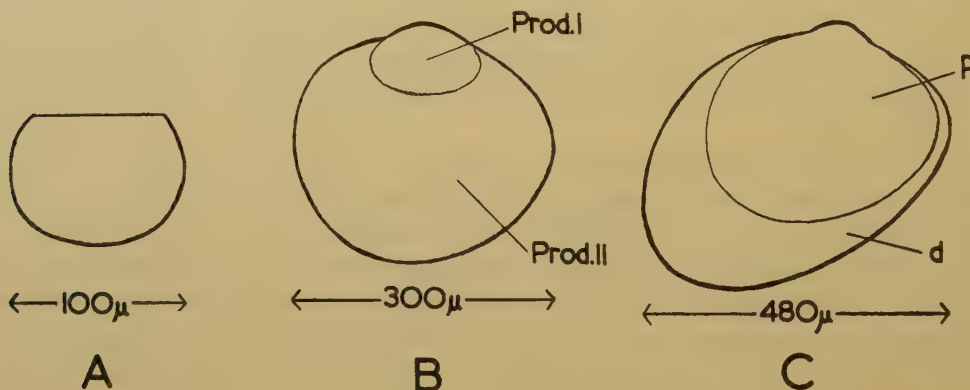


## TERMINOLOGY.

The *length* of a larva is the longest distance in a direction roughly parallel to the hinge. Unless otherwise indicated all measurements given in this paper are of length (in  $\mu$ ). *Breadth* (broad, narrow) is the distance from the tip of the umbo to the ventral margin. *Convexity* (convex, flat) is a measure of the maximum distance through the bivalve from side to side.

Looking at a valve from the side (when only one valve of the bivalve can be seen) the dorsal margins are immediately on either side of the umbo. The remainder of the margin is made up of the two ends and the ventral margin. All these margins, of course, normally merge into each other.

The following terms in *italics*, used later in this paper, have been fully defined by Werner (1939).



TEXT-FIG. 1.—A.—Veliger = “D-shaped larva” = “straight-hinge stage.”

B.—Veliconcha made up of prodissoconch I (Prod. I) and prodissoconch II (Prod. II).

C.—Early bottom-living stage showing prodissoconch (*p*) and dissoconch (*d*).

The trochosphere passes into a bivalve *veliger* (Text-fig. 1A). In the restricted sense of the term as used by Werner (1939), this corresponds to the “D-shaped larva” or the “straight-hinge stage” of previous authors. In particular, the veliger has no hinge differentiation whatsoever. After a pause the final larval shell is laid down and the larva becomes a *veliconcha* (Text-fig. 1B). The D-shaped veliger shell (*prodissoconch* I) is usually distinctly marked off from the veliconcha shell (*prodissoconch* II). After spatfall and metamorphosis the definitive adult shell (*dissoconch*) is laid down, but the prodissoconch is usually clearly marked off (Text-fig. 1C).

## MEANS OF IDENTIFICATION.

Identification is based entirely on the shell, primarily on its shape and on the structure of the hinge, with texture being used whenever it is sufficiently distinctive. Shape and hinge structure must have reached a sufficient degree of

development, *i.e.* well into the veliconcha stage. The veligers must as yet be considered unidentifiable though efforts have been made, notably by Werner (1939), to identify a few of them by ratios derived from the hinge length, shell length and breadth. It is hardly likely, however, that trustworthy unique ratios would be found for each of, say, 100 species. In any case, unless one is prepared to go back as far as the egg, one must decide on a suitable stage in development and identify to species only individuals larger than that stage. It is sought here to identify only those larvae whose shape and hinge structure are sufficiently differentiated to allow identification by general appearance. The minimum size allowing identification by general appearance undoubtedly varies with different species and, quite possibly, with different workers.

### *Shape.*

It is a useful rule that the shapes of allied species are variations of a shape characteristic for the group of species. However, two or more groups of allied species may have a similar basic shape so that classification by this character alone cannot usefully be taken very far. Sullivan (1948), for example, classifying by shapes, has grouped together such widely different genera as *Ensis*, *Mytilus*, *Rochefortia* (*Kellia*) and *Venus*. This may be empirically useful in a given locality with a limited number of species, but it fails in universal application.

The three features to be considered are the shape of the shell margin, the prominence of the umbones, and the convexity of the larva. Indication of basic shapes of various groups will be given later, but the best idea of these can be obtained from the grouped photographs (Plates I-V). An appreciation of the basic shapes is essential for easy identification.

The commonest general shape of larvae is that in which one end is broad (or more produced) and the other end narrow. This is, in many cases, rather a loose description but clear enough in practice. In Table I, it is stated of each group, when possible, whether the broad end is anterior or posterior thus allowing orientation of the larvae of the group, though orientation does not greatly matter for identification.

### *Position of Ligament.*

The position of the larval ligament (Text-fig. 2, *lig.*) can be useful both in identification of the basic hinge type and in the orientation of the larvae of the group. It is external in the Solenacea and internal in all other groups. When internal it is situated in relation to the straight hinge part (see below), in most cases away from the centre of it and towards the broad end of the larva. Its position, when possible, is indicated for each group in Table I.

### *The Hinge Apparatus.*

The function of the hinge is to ensure that the valves meet exactly on closure and to ensure that the valves do not slide on each other under uneven pressures

(Dall, 1895). The hinge apparatus, consequently, increases in strength and often in complexity as the larva gets larger, and is roughly proportional to the weight of the shell. In some superfamilies there is no great change in complexity with increasing size (within the identifiable range), only an increase in the strength of the component parts (*e.g.* Saxicavacea, Adesmacea). In other superfamilies new structures are laid down as the larva increases in size (*e.g.* Tellinacea, Mac-tracea). In seeking relationship between hinge structures this fact has to be remembered; only hinges that have reached the same stage in development should be compared. Since the hinge serves a necessary function in the life of pelagic larvae there is always some hinge differentiation in *pelagic* larvae above a certain size (say  $150\mu$  or even smaller).

The hinge of every larva investigated has agreed with one of eighteen basic types listed in the left-hand column of Table I. Fourteen correspond to single superfamilies, one corresponds to the Pteriacea and Ostreacea combined (these are combined by Haas (1926) into the suborder Schizodonta), and one to the Pectinacea and Anomiacea combined (combined by Haas into the suborder Iso-donta). For the remaining two types the two families of the Myacea are separated and the Myidae joined with the Saxicavacea to give one type, the Alroididae remaining alone to give the other. Haas (1926) does not recognize a superfamily Saxicavacea but joins the Myidae, Corbulidae (= Alroididae), Saxicavidae and Gastrochaenidae into the superfamily Myacea.

All superfamilies with representatives in the North Sea are thus accounted for except the Nuculacea, which have peculiar larva and are recognizable without reference to hinge (see p. 89), the Isocardiacea, which has one species limited to the English coast, and the Gastrochaenacea,<sup>1</sup> with one species limited to the Belgian coast.

The basic types are shown in Text-fig. 3 and the hinge features of each group summarized in Table I: the table should be read in conjunction with the supplementary notes. Before dealing with the hinge of each group, however, it is necessary to explain how the hinge is constructed and the meaning of the various terms used in Table I and the supplementary notes. The various parts to be described are shown in Text-fig. 2.

The two valves of a small bivalve larva meet all round in one plane. A portion of the margin is straight and the straight parts of the two valves remain in contact when the larva gapes; if there were no straight parts there would be only point contact at gape. The straight parts persist throughout larval development though, in a few cases, there may be a curving from the plane of part of the remaining margin as the larva gets larger.

The portion of the shell forming the straight part of the valve may thicken to form a *provinculum* (Bernard, 1898) (Text-fig. 2, *prov.*). The *provinculum*

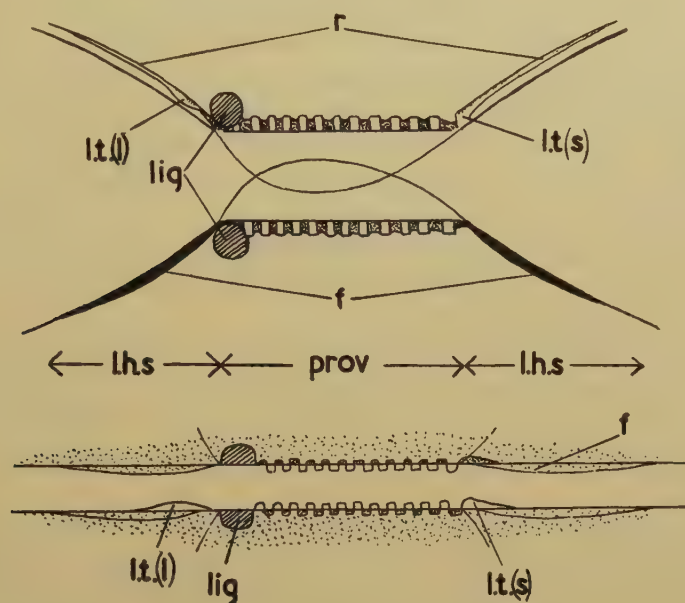
<sup>1</sup> It is possible that *Gastrochaena* has a hinge similar to that of the Saxicavacea since Haas (1926) includes it under the Myacea.



always bears teeth (*the provincular teeth*) or is moulded into tooth-like projections. Hinge structures, apart from special teeth, present beyond the limits of the provinculum constitute the *lateral hinge system* (Text-fig. 2, *l.h.s.*).

The fully-developed hinge apparatus may, therefore, consist of two parts, the provinculum and the lateral hinge system, together with the *special teeth*.

*The provinculum.*—(Text-fig. 2, *prov.*). By definition, if there are any teeth or tooth-like projections beneath the straight part of the shell margin a provinculum is present and a provinculum is, in fact, present in all groups except two, the Lucinacea and Erycinacea.



TEXT-FIG. 2.—A diagrammatic drawing of the inside (above) and dorsal (below) views of a larval hinge to show the various components: *f.* = flange; *l.h.s.* = lateral hinge system; *lig.* = ligament; *lt.(l)* = lateral tooth (lamellar); *lt.(s)* = lateral tooth (solid); *prov.* = provinculum; *r.* = ridge.

Provincular structures may be divided into four types:

Type *a.*—There are several or numerous rectangular teeth in each valve, easily seen on inside view of the hinge. This is the type illustrated in Text-fig. 2. These teeth may be regular or irregular in arrangement and equal or unequal in size.

Type *b.*—There are one, two or three strong rectangular teeth in each valve, easily seen on inside views (*e.g.* Saxicavacea, Text-fig. 3).

Type *c.*—There are projections on a thin provinculum. These are not easily seen on inside view, but are quite distinct on dorsal view of the hinge (*e.g.* Pandoracea, Text-fig. 3). This type is probably not essentially different from Type *b*, the latter consisting of projections on a thick provinculum.

Type *d*.—There is a thin strip of very small, spiky or tubercular teeth which, on closure, are inserted into gaps on the other valve, which does not have similar spiky teeth. This type is usually superimposed on provincular structures of Types *b* and *c* (e.g. Cardicea, Text-fig. 3).

*The lateral hinge system*.—(Text-fig. 2, *l.h.s.*). When present this consists of lateral flanges and calcareous ridges. In some cases projections, referred to as lateral teeth, develop from the calcareous ridges.

When most larvae are opened out and viewed from the inside, it will be seen that one valve (the left) has thicker dorsal edges than the other. The right valve has thin dorsal edges, but an internal calcareous ridge (Text-fig. 2, *r.*) runs more or less parallel to each edge, on either side of the umbonal region. The reason for this is seen when the valves are viewed dorsally. Projecting outside the margin from the dorsal edges of the left valve are flanges (Text-fig. 2, *f.*) which, when the bivalve is closed, underlap the edges of the right valve.

Flanges are present in most groups and usually, but not always, both the flanges, one anterior and one posterior to the umbo, are on the same valve. The calcareous ridges occur on the other valve, *i.e.* they occur in such a way as to appear to act as stops to the flanges.

At the extreme ends of the straight hinge part of the valve with ridges there may be tooth-like projections, to be seen most clearly in dorsal view. These may, at first, be taken as provincular teeth but are, in fact, developments of the calcareous ridges, and therefore part of the lateral hinge system, *i.e.* lateral teeth (Text-fig. 2, *l.t.*).

Two types of lateral teeth can be distinguished both by structure and function. One type is a lamina (Text-fig. 2, *l.t.(l)*), developed from the calcareous ridge, which underlaps the rim of the opposite valve and does not come into contact with any part of the provinculum of the other valve. The other type, also a development of the ridge, is more solid and comes in contact with the outside edge of the provinculum of the other valve on closure (Text-fig. 2, *l.t.(s)*).

Commonly the flanges narrow gradually towards the provinculum (Text-fig. 2) but, in some cases, the flange ends abruptly or even projects at the provincular end, thus giving the impression of a tooth. However, by the present definition, these abrupt terminations or projections are considered to be part of the flanges and not teeth (see p. 86).

*Special teeth*.—Special teeth are limited to four groups and need no description here. They are projecting teeth which cannot readily be referred either to the provincular or lateral hinge systems.

#### *The Hinge Characters of Each Group.*

Now that the generalized hinge structure has been defined we can consider how the various parts are combined to give each basic type. Hinges develop

with increasing size, and not every stage in development in each case can, as yet, be described, but the object is to enable identification at some stage; once that is successfully done the identification of smaller and larger larvae of the same species is relatively easy.

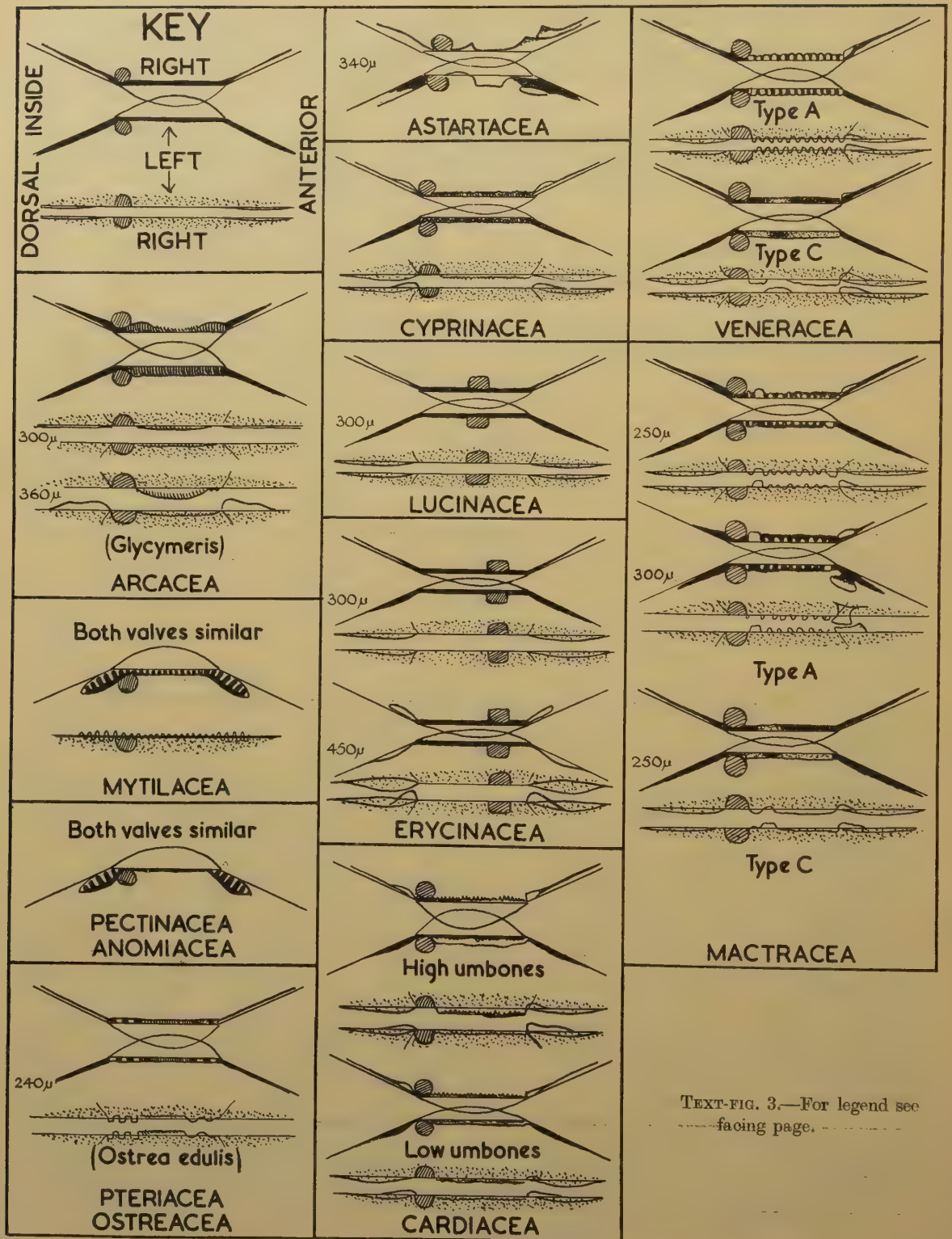
The 18 basic types are shown in Text-fig. 3, and the features summarized in Table I. The additional notes below are meant to clarify the figures and table. The orientation of the valves is given by a key figure in Text-fig. 3.

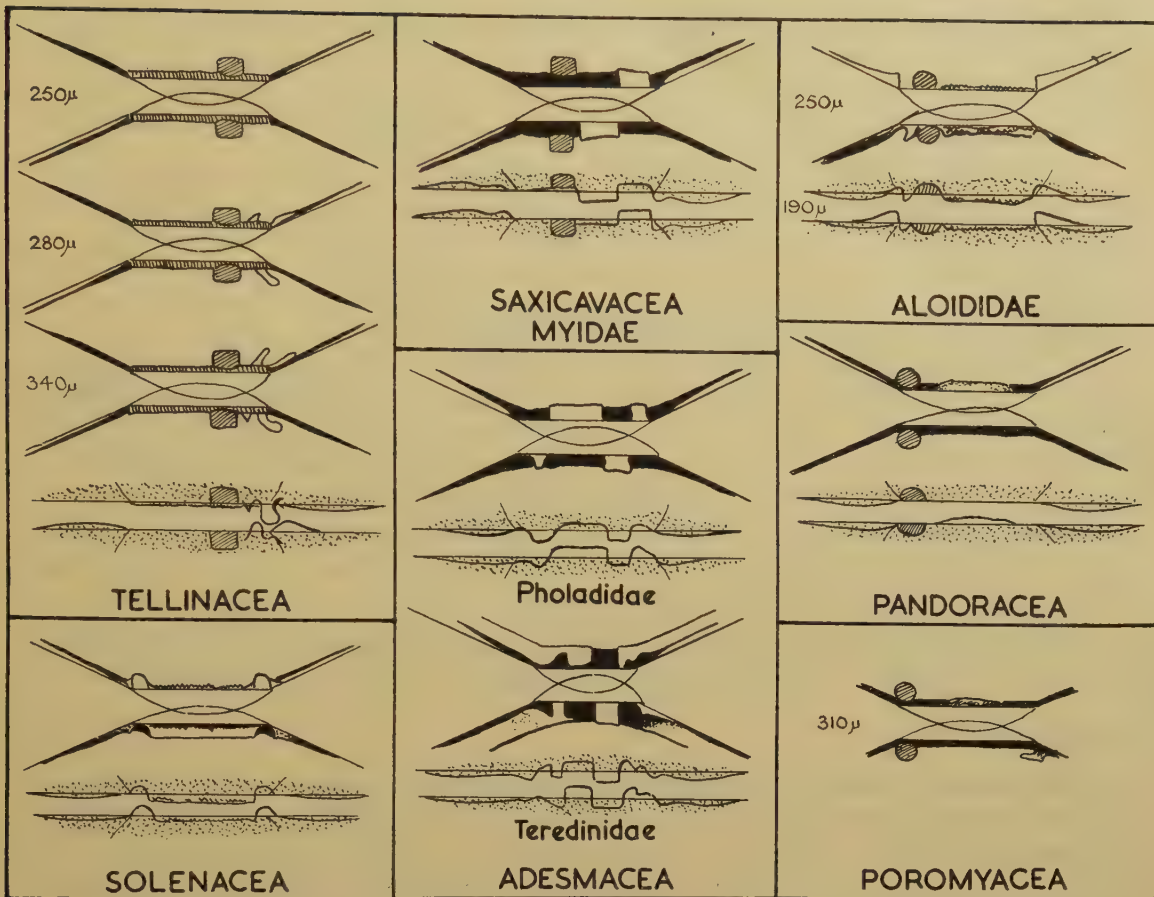
TABLE I.—*Summary of Larval Features in Each Group except Nuculacea, Isocardiacea and Gastrochaenacea.*

$X$  = present;  $-$  = absent;  $?$  = no information;  $A$  = anterior;  $P$  = posterior;  $Q$  = equilateral valves;  $C$  = centre;  $L$  = left valve;  $R$  = right valve;  $E$  = external;  $l$  = lamellar;  $s$  = solid;  $a, b, c, d$ , = types listed on p. 79.

|             |   | Broad side. | Ligament. | Provincular teeth. |   | Flanges |      |   | Lateral teeth |      | Special teeth. |
|-------------|---|-------------|-----------|--------------------|---|---------|------|---|---------------|------|----------------|
|             |   |             |           |                    |   | $A.$    | $P.$ |   | $A.$          | $P.$ |                |
| Arcacea     | . | $A$         | $P$       | $a$                | . | $-$     | $-$  | . | $X$           | $X$  | $-$            |
| Mytilacea   | . | $P$         | $P$       | $a$                | . | $-$     | $-$  | . | $-$           | $-$  | $-$            |
| Pectinacea  | } | $P$         | $P$       | $a$                | . | $-$     | $-$  | . | $-$           | $-$  | $-$            |
| Anomiacea   |   |             |           |                    | . |         |      | . |               |      |                |
| Pterinea    | } | $Q$         | $P$       | $a$                | . | $-$     | $-$  | . | $-$           | $-$  | $-$            |
| Ostreacea   |   |             |           |                    | . |         |      | . |               |      |                |
| Astartacea  | . | $?$         | $?$       | $b$                | . | $?$     |      | . | $?$           |      | $X$            |
| Cyprinacea  | . | $P$         | $P$       | $d$                | . | $L$     | $L$  | . | $l$           | $l$  | $-$            |
| Lucinacea   | . | $A$         | $C$       | $-$                | . | $L$     | $L$  | . | $l$           | $l$  | $-$            |
| Erycinacea  | . | $A \& Q$    | $A$       | $-$                | . | $L$     | $L$  | . | $l$           | $l$  | $-$            |
| Cardiacea   | . | $P$         | $P$       | $b, c + d$         | . | $L$     | $L$  | . | $s$           | $l$  | $-$            |
| Veneracea   | . | $P$         | $P$       | $a, c$             | . | $L$     | $L$  | . | $s$           | $-$  | $-$            |
| Mactracea   | . | $P$         | $P$       | $a, c$             | . | $L$     | $L$  | . | $X$           | $-$  | $X$            |
| Tellinacea  | . | $A$         | $A$       | $a$                | . | $L$     | $R$  | . | $X$           | $-$  | $X$            |
| Solenacea   | . | $P$         | $E$       | $b + d$            | . | $L$     | $L$  | . | $-$           | $-$  | $-$            |
| Saxicavacea | } | $P$         | $P$       | $b$                | . | $L$     | $R$  | . | $-$           | $-$  | $-$            |
| Myidae      |   |             |           |                    | . |         |      | . |               |      |                |
| Aloididae   | . | $Q$         | $P$       | $b + d$            | . | $L$     | $L$  | . | $s$           | $s$  | $-$            |
| Adesmacea   | . | $Q$         | $P$       | $b$                | . | $L$     | $L$  | . | $-$           | $-$  | $-$            |
| Pandoracea  | . | $P$         | $P$       | $c$                | . | $L$     | $L$  | . | $-$           | $-$  | $-$            |
| Poromyacea  | . | $Q$         | $?$       | $c$                | . | $?$     |      | . | $?$           |      | $X$            |







TEXT-FIG. 3 (cont.).—Figures showing the 18 basic types of hinges comprising all groups of North Sea lamellibranchs, with the exception of the Nuculacea, Isocardiacea and Gastrochaenacea, as described in the text. Where hinges increase in complexity with size of larva the approximate larval size is indicated against the hinge. Orientation is shown in a key figure at the top left corner of the facing page.

#### Arcacea.

The position of the ligament towards the narrow (p. 77) end is exceptional.

*Provinculum*.—The teeth are numerous, very small and more or less equal in size. In dorsal view they appear to be roofed over and not all separated by clear gaps.

*Ridges*.—Ridges are present in the smaller larvae.

#### Mytilacea.

*Provinculum*.—The term provinculum here is extended to include the thickening of the shell beyond the limits of the straight hinge section since this lateral thickening is quite unlike anything to be found in the usual lateral hinge system. It is also historically correct to use the term here to cover the whole hinge system (Bernard, 1898).

The region between the two most thickened parts bears teeth which are easily visible.

Pectinacea and Anomiacea (the Isodonta of Haas, 1926).

*Provinculum*.—This is very similar to that of the Mytilacea, but the region between the two most thickened parts is so thin that teeth are absent or extremely minute.

Pteriacea and Ostreacea (the Schizodonta of Haas, 1926).

*Ligament and Provinculum*.—The teeth consist of a strip of roofed-over taxodont teeth and, posterior to this strip, a few bigger rectangular teeth with clear gaps in between. In *Ostrea edulis*, at least, there are some large corrugations anterior to the taxodont teeth, but these are not included in this definition of the hinge type (see p. 92). According to Bernard (1898) and Borisjak (1909) the ligament lies between the taxodont strip and the posterior rectangular teeth.

Astartacea.

No further information is available apart from the drawing of a large larva (340  $\mu$ ) in Text-fig. 3. The large special tooth of the left valve is spatulate.

Cyprinacea.

*Provinculum*.—It is doubtful whether this should be regarded as a Type *d* only or a combination of Types *c* and *d* as in the low-umboned species of the Cardiacea.

Lucinacea and Erycinacea.

These are the only two groups without a provinculum.<sup>1</sup> The straight edge of very large larvae of some species may appear on inside view rough or corrugated, giving the impression of feebly-developed teeth. In such deceptive cases the dorsal view is decisive; no structures project beyond the shell margin in the region of the straight part (*cf.* the dorsal views for these two superfamilies with those for all other types shown in Text-fig. 3).

As far as is known the only difference in the hinges of the two groups is that the ligament is central, or possibly posterior to centre, in the Lucinacea and anterior to centre in the Erycinacea.

Cardiacea.

*Provinculum*.—In the right valve the provinculum is very thin and consists of a strip of spiky teeth. The provinculum of the other valve is thicker and

<sup>1</sup> This statement may not be true for large larvae ( $> 300\mu$ ) of the Lucinacea but it is, in practice, adequate since in all other groups normally pelagic larvae have a provinculum at a size of  $200\mu$  upwards. Too few larvae of the Lucinacea have been obtained for full definition.



projects as a long tooth with gaps along its dorsal inside edge for the reception of the spiky teeth. The detail of this structure is best made out in the high-umboned larvae; in the low-umboned larvae the provinculum is built on a smaller scale making the detail difficult to appreciate.

#### Veneracea.

*Provinculum*.—In the Type *c* hinge the projections may be rough and give an impression of numerous incipient teeth on inside view. In dorsal view the constant feature of this type is a long projection on the anterior of the left valve which is apposed to the solid lateral tooth of the right valve on closure. There are other projections.

#### Mactracea.

*Provinculum*.—The two types are very similar to the two of the Veneracea. In most species of Mactracea of Type *a*, however, one of the rectangular teeth towards the posterior of the right valve is prominent and distinctive (see p. 95).

*Special tooth*.—A special tooth arises from about the size of  $270\mu$ . This becomes a well-developed spatulate tooth which is pressed ventrally against the lateral tooth, which has formed earlier, when the larva is closed.

#### Tellinacea.

*Provinculum*.—There is a series of tiny, rectangular teeth which resemble the taxodont type when viewed towards the inside.

*Ridges and flanges*.—Like the Saxicavacea, and unlike all other groups, these alternate, one flange on the right valve and the other on the left.

*Special teeth*.—These arise in succession with increasing size of larvae (see Text-fig. 3).

#### Solenacea.

*Ligament*.—The ligament is external but does not appear till late ( $> 270\mu$ ).

*Provinculum*.—On the left valve there is a rectangular tooth reaching nearly the full length of the provinculum, and on the right valve a small tooth at each end of the provinculum. Above a certain size (*ca.*  $340\mu$ ) one of the two small teeth increases in length (Text-fig. 4). The system of spiky teeth is very like that of the Cardiacea.

#### Saxicavacea and Myidae.

*Provinculum*.—There is one strong provincular tooth in each valve. In the low-umboned species (*Mya*), which have a thin provinculum, these teeth may almost be described as merely projections.

*Ridges and flanges*.—These alternate as in the Tellinacea,

### Aloididae.

*Provinculum*.—The system of spiky teeth is very like that of the Cardiacea. In the left valve there is a distinct tooth posterior to the ligament, constituting one side of the gap that receives the posterior solid tooth of the right valve.

### Adesmacea.

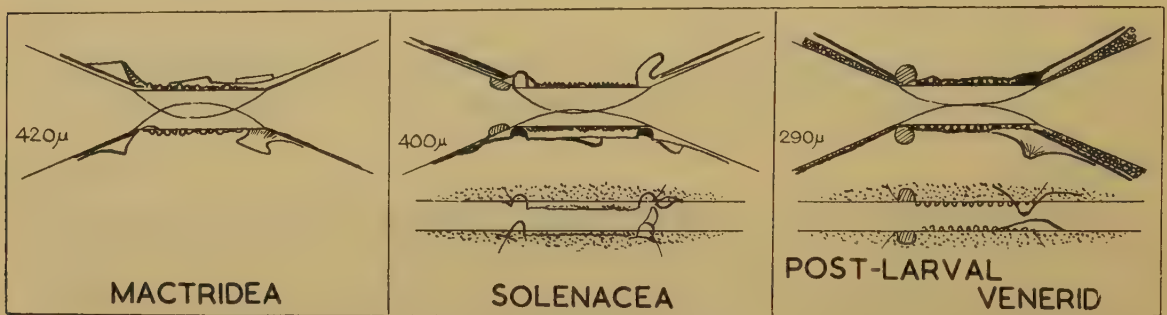
*Provinculum*.—The Pholadidae can be distinguished from the Teredinidae by the fact that the central tooth is much longer in the former.

### Pandoracea.

*Provinculum*.—There is a long projection on the right valve and none on the left.

### Poromyacea.

No further information is available apart from the drawing shown on Text-fig. 3. At  $300\mu$  the hinge has a distinctive special tooth.



TEXT-FIG. 4.—The hinges of unusually large Mactracean and Solenacean larvae and of a post-larval Venerid.

Following the policy of keeping the description of the hinge as simple as possible, lateral teeth have been defined as developments on valves without flanges, *i.e.* as developments of the calcareous ridges only. Any thickening forming a tooth at the provincial end of the flanges has been neglected. However, such “flange teeth” occur in the Saxicavacea (and Myidae) and possibly the hinges of the Adesmacea could be more exactly defined if this extra component was recognized.

Dall (1895) combined the Veneracea, Tellinacea, Solenacea and Mactracea into the Teleodonta. Special teeth have been shown (Text-fig. 3) in the Tellinacea and Mactracea and it would be of interest to see if there was a similar development of special teeth in the two remaining superfamilies. In Text-fig. 4 hinges of unusually large Mactracean and Solenacean larvae are shown, together with the hinge of a Venerid specimen in which the dissoconch had begun to form (prodissoconch  $250\mu$  in an overall length of  $290\mu$ ).

### Texture.

The nature of the concentric lines and similar sculptural features, the strength or fragility of the shell, and the colour of the shell (not of the soft parts) are useful

features for the identification of larvae. Unfortunately these features are inadequately illustrated in the plates, but outstanding textures are mentioned in the descriptive part.

Texture changes with increasing size. Thus it is common for shells to be relatively strong at small sizes and fragile at large sizes. Colour, if present, increases in intensity with size. Unless otherwise stated the texture described in the text is that of the larger larvae illustrated.

Allied larvae tend to have similar texture.

When a larva has been identified by the shell shape and the hinge, the texture should be observed as it will be found that this is of assistance in subsequent routine examinations of plankton samples. Once the species of larvae have been learnt they are recognized by their general appearance, by their shape and texture.

### THE SPECIFIC IDENTIFICATION OF LARVAE IN THE NORTH SEA.

The surest method of determining the species of a larva is by culturing. In the present investigation no culturing has been done and the identification is consequently indirect. It is therefore necessary to indicate the indirect sources that have led to specific identification, apart, of course, from the available literature on the subject.

That a natural classification of larvae is possible is of very considerable help. This has been the most fruitful of the indirect sources and brings the larva down to a short list, sometimes a very short list, of species. For example, a larva can be placed in the Solenacea without doubt. There are, it appears, only four species of this superfamily in the North Sea (Haas, 1926) so that the larva can be only one of these four, thus eliminating well over 100 other species.

Of some, but limited, use is the postulate that in a group of allied species the differences between the larvae are reminiscent of the differences between the adults. This has been applied, for example, to the species of *Abra*.

Specific identification is often possible through the agreement between the distribution and frequency of a larva and the known distribution of the adults.

One further aid to identification is the fact that the larval shell (prodissoconch) is usually marked off at the umbo from the definitive shell (dissoconch) in young bottom-living bivalves (Text-fig. 2). On the whole it has not seemed possible to identify larvae to species by the shape of the prodissoconch, but it is possible to obtain an indication of the type of shape to be expected of the larvae of the genus.

Two limitations to this process of indirect identification may be mentioned. Firstly, the lamellibranch fauna in the area being worked must be thoroughly known and it can hardly be claimed that this is the case over the whole North Sea. Secondly, there is not universal agreement on the specific status of some forms, particularly in the Mactracea. Eventually the larvae should help to clarify the



position. In the meantime, however, this doubt about the specific status of some forms makes indirect identification more difficult.

Altogether 77 pelagic larvae have been described in the following part. Haas (1926) lists over 120 species occurring in the North Sea proper (*i.e.* excluding forms limited to the coast). Some of these are known to have non-pelagic larvae, accounting for at least another 16 species (including the Nuculacea) and, with our present knowledge of the hinge, six additional species can be identified from previous literature. The fitting of larvae to species has in many cases been speculative and a convention has been adopted giving three degrees of certainty. When there is confidence the name is given directly, *e.g.* "*Mytilus edulis*." When there is doubt the larva is lettered and the specific name given in brackets with a question mark *e.g.* "PHOLAD A (? *Pholas dactylus*)"; when the specific name cannot be suggested the larva is lettered only, *e.g.* "PECTINID D."

There has been no hesitation in publishing descriptions of larvae which, as yet, cannot be assigned to species. The most serious lack in our present knowledge is how, and by how much, allied species differ and this question must be settled before confident specific identification can be made. For example, the larva of *Mytilus edulis* has been described about 10 times. Yet Jørgensen (1946) undoubtedly described a mixture of *Mytilus edulis* and *Modiolus modiolus* under the former species, and Lebour (1947) identified larvae as "*Mytilus* or relative." The apparent uncertainty in the identification of *Mytilus* larvae is due to ignorance of the extent of inter-specific differences; are the larvae of *Modiolus barbatus*, for example, so like those of *Mytilus edulis*, that there is uncertainty in the identification of *Mytilus edulis*? In consequence, every additional Mytilid larva which is described and shown to be recognizably different from *Mytilus* larva increases the certainty in identification of *Mytilus*, even though the species of the newly-described Mytilid may not be known. The identification of lamellibranch larvae is a process of comparison and contrast.

It is not certain that all the larvae described below are truly pelagic. Spat forms, which can easily be distinguished from larvae, are occasionally found in the recorder material. Presumably these have been brought up from the bottom in turbulent water, and it is possible that non-pelagic larvae, which have not been distinguished from pelagic larvae, have also been brought up in the same way and collected by the recorder. Such a possibility is mentioned below in the consideration of two larvae (*Astarte* sp. and *Gari fervensis*). Even allowing the possibility of one or two others, however, the total effect must be of little importance.

Since most of the species of larvae have been identified by indirect means there may well be errors in the identification. Readers who recognize such errors, or who can give information on the doubtful and unidentified larvae, are asked to inform the author so that these revisions can be included in a later report.

A detailed description of each form is unnecessary. When an unrecognized larva is found the first step is to determine its type of hinge. The hinge of a larva

may differ in detail from one of the basic types shown in Text-fig. 3, but there should be no difficulty in deciding that a particular hinge belongs to one basic type, and no other. Once the type has been decided the next step is to try and fit the shape of the larva to one of the photographs, grouped according to hinge types, in the plates. If a fit is obtained, the description in the text should be checked.

On the whole the descriptions need only include texture since the photographs usually give all the necessary information on shape. In most larvae the concentric lines of the shell are fine and close-set. If, therefore, no comment is made on the concentric lines it can be assumed that they are of this character.

Some of the larvae have been obtained very rarely and indication of the number of specimens is given in brackets immediately before the descriptions, thus (1), (2), (+) a few, (++) many, (+++) very many.

## ORDER TAXODONTA.

### Superfamily Nuculacea.

[For references see Jørgensen, 1946.]

The Nuculacea are probably all either non-pelagic or pelagic only for a very short time (say three or four days), the pelagic larvae being surrounded by large velar cells giving a barrel-shaped structure (Drew, 1899 and 1901). No members of this superfamily have been identified in our material.

### Superfamily Arcacea.

Three species are shown in Plate 1.

*Glycymeris glycymeris* (Linné) (++)—This is an easy larva to recognize at a size of 360–420 $\mu$ . The shell is strong and heavy, and the pallial line which runs parallel and close to the margin of the shell is very distinct.

The hinge has been described in general terms on p. 83. In the left valve of this species the ventral edge of the strip of teeth, as seen inside, is straight and smooth, whilst in the right valve the ventral edge is jagged (Text-fig. 3).

Distinct from the hinge apparatus there is, in the left valve, a shallow rim which encircles the whole valve except at the hinge, and for a small arc of about 5°. This rim underlaps the margin of the right valve which has an internal calcareous ridge corresponding to the rim. Thus there is a pill-box arrangement. The internal ridge starts on either side of the umbo and extends about half-way round at a size of about 340 $\mu$ .

Lateral ridges, comparable to those of other species, are present in smaller specimens.

The species is probably incubatory in the earlier larval stages, and pelagic stages smaller than 260 $\mu$  have not been recognized.

ARCACEAN A (1).—The hinge is basically like that of *Glycymeris* but without the distinctive jagged edge to the taxodont strip. The shell is strong, with a pill-box system.

ARCACEAN B (? *Limopsis* sp.) (+).—This has a thinner shell than the above two species and the hinge is simpler. Large specimens have the pill-box system.

The appearance, structure and distribution of the first described larva can leave little doubt that it is of *Glycymeris*. However, the prodissoconchs at the umbones of five small bottom-living specimens of *Glycymeris* (4–8 mm.) provided by Dr. Stephen were quite different, these forming very distinct caps 170–210 $\mu$  across. Outside the cap the shells had growth lines with no distinct area marked off, but the run of the lines near the umbo clearly resembled



the described larvae. Similarly, there was a distinct cap about  $160\mu$  across on three bottom-living specimens of *Limopsis aurita* (Broochi). On two specimens there was no other clear area marked off, but on the third there was an area  $320\mu$  across shaped not unlike the larva tentatively referred to *Limopsis* (ARCACEAN B). Whilst Haas (1926) lists only *L. aurita* in the North Sea Schrader (1911) recorded *L. minuta* (Phil.) also.

## ORDER ANISOMYARIA.

### Superfamily Mytilacea.

[For references see Jørgensen (1946): in addition Sullivan (1948) has described *Mytilis edulis* and *Modiolus demissus* (Dillwyn)]. Members of this family are easily recognized by the hinge. The only other type of hinge which has any resemblance to it is that of Pectinacea. Nine species are shown in Plate I.

*Mytilus edulis* Linné (+++).—Nelson (1928) gives good photographs of bivalve larvae. Jørgensen (1946) refers to a wide variation in shape and colour and later suggests that the resemblance between this species and *Modiolus modiolus* is so close that a confusion of the two species may have taken place. It is believed that this has, in fact, occurred, but that the variation he mentions is a function of size. Larvae of the two species, all of the same size (not too small), are quite distinct. *Mytilus* is described in comparison with *Modiolus*.

*Modiolus modiolus* (Linné) (+++).—In the smaller specimens of *Mytilus* and *Modiolus* the shape is similar, though the narrow end is more pointed in the latter. In later stages the two shapes become more differentiated, the more pointed end of *Modiolus* remaining a distinctive feature and, in addition, the broad end of the same form droops ventrally and backwards, to a degree considerably more than in *Mytilus*, size for size.

The smaller specimens of the two species are more easily separated by their texture than by shape. The shell of *Modiolus* is a much stronger one than *Mytilus*, and, correspondingly, the hinge is relatively more massive, the umbo more pronounced, the concentric lines more distinct. The empty shell, too, is more strongly coloured, flaxen, particularly on the ventral side. In the intact bivalve, *Modiolus* is more opaque than *Mytilus*. Probably Jørgensen's drawing (his Fig. 167B) is of *Modiolus modiolus*.

An interesting feature is that in both species the dorsal shoulder of the broad end is separated from the main body by a very shallow furrow. This furrow is fairly distinct in single valves above  $300\mu$  but indications of it may be seen in small forms, even at  $200\mu$ .

*Musculus marmoratus* (Forbes) (+).—Described by Jørgensen (1946). Figs. 11 and 12 of Odhner (1914) are certainly of this species. The shell may be imagined as a *Modiolus* shell shortened dorso-ventrally. It is recognizable at  $150\mu$ , possibly earlier.

*Adula simpsoni* Marshall (+).—This has a strong shell with a rich brown colour. The concentric lines are very distinct and moderately set. A comparison of this larva with adults of *A. simpsoni*, collected by Dr. Stephen, has left no doubt about the correctness of the identification.

MYTILID A (++).—The shell is firm, like *M. modiolus*, but the concentric lines are fine and close set. The main part of the shell is colourless but in large forms ( $>300\mu$ ) the rim is yellowish and usually the dorsal margins are rose coloured. The umbo is low. A specimen measuring  $380\mu$  has been found.

MYTILID B (1).—The umbo is very low. The shell is rather thin and strongly coloured a yellow brown with rose along the dorsal margins, more strongly coloured than *M. modiolus* and much more so than *M. edulis*.

MYTILID C (2).—The shell is fragile and nearly colourless, with very indistinct concentric lines.



MYTILID D (1).—The shape is very distinctive with a break on either side of the umbonal region. The shell is strong but the concentric lines are very indistinct.

MYTILID E (? *Crenella* sp.) (1).—The shape is almost equilateral and the umbo low. The shell is colourless.

Jørgensen (1946) records that the size of the prodissoconch of a bottom stage of *Crenella decussata* (Montagu) was 750 $\mu$ . On two specimens, provided by Dr. Stephen, there is a non-decussated area about 600 $\mu$  across within which a line delimits an area 290 $\mu$  across. It is possible that it is the smaller area which corresponds to the prodissoconch. Outside this the non-decussated area may be an interdissoconch as described by Jørgensen (1946) in *Musculus marmoratus* where the shell characteristic of the species does not form until the spat is 1 mm. in length. The shape of MYTILID E certainly suggests that it is a larva of *Crenella*.

Of the other unidentified larvae, MYTILID A may prove to be *Modiolus phaseolinus* (Philippi).

*Musculus discors* (Linné) and *Musculus niger* (Gray) have non-pelagic larvae (Thorson, 1935).

### Superfamily Pectinacea.

[For references see Jørgensen (1946)]. Only Jørgensen has described larvae, within the identifiable range, of any North Sea species of *Pecten* (*Chlamys*). Five species of the Pectinidae and one of *Lima* are shown on Plate I.

*Chlamys striata* (Müller) (1).—This has been described by Jørgensen (1946).

PECTINID B (+).—This is slightly inequivalve. The more convex valve curves deeper towards the other valve at one place, with a corresponding retraction of the margin of the other valve. This curvature of the margin gives a characteristic slight concavity in the outline of the ventral edge. The shell is tough with a strong flaxen colour towards the ventral edge. Towards the margin the concentric lines are well marked and set moderately apart. No specimens over 220 $\mu$  in length have been seen.

PECTINID C (+).—The shell is thin and coloured. A specimen measuring 280 $\mu$  has been found.

PECTINID D (+).—Equivalve. One specimen has a fringe of dissoconch shell on one valve and had therefore just undergone metamorphosis at a size of 220 $\mu$ .

PECTINID E (+).—The two specimens shown on Plate I are believed to be of the same species but this is not certain. The larvae are equivalve and have thin shells.

For the present we cannot go far with the specific identification of the above larvae, especially as 13 species are listed as occurring in the North Sea. Of these we can possibly eliminate *Chlamys similis* (Laskey) since the prodissoconch of bottom-living specimens measures only 125–150 $\mu$  (Jørgensen, 1946). On a single bottom specimen of *C. distorta* (da Costa) the prodissoconch measured less than 200 $\mu$ .

*Lima* sp. (++).—The photograph is sufficiently similar to the drawing of *Lima loscombi* Sowerby (Jørgensen, 1946) to make such a specific identification probable. The shell is firm and colourless.

### Superfamily Anomiacea.

[For references see Jørgensen (1946)]. Sullivan (1948) gives photographs of small larvae, before the pedal sinus is formed, and it will be seen from these that the genus, at least, can be recognized in quite small specimens. Three species are shown on Plate I.

*Anomia ephippium* Linné (++).—Described by Odhner (1914) whose drawing is excellent. This is distinguished from the following species by the slight shoulder on the dorsal side of the broad end. This is more obvious in the complete larva than in the single shell.

*Heteranomia squamula* (Linné) (++).—Described by Stafford (1912), Lebour (1938b) and Jørgensen (1946). The broad end in this falls away directly from the umbo.

*Monia squama* (Gmelin) (1).—This has a stronger shell than either of the above and the concentric lines are well marked. At 230 $\mu$  there is a distinct lump towards the ventral side of the broad end leading to a distortion of the concentric lines. There is, also, a smaller lump opposite it on the flat valve.

The only other species listed in the North Sea is *Monia patelliformis* (Linné) and, according to Bernard (1896), this larva has a pedal sinus in both valves.

### Superfamily Pteriacea and Ostreacea.

The definition of the hinge type is based not only on personal observations of the hinge of *Ostrea edulis* (Linné) (Text-fig. 3), but also on the description by Bernard (1898) and Borisjak (1909) of *Ostrea* and *Pinna* hinges. The definition given is limited to the series of Arcacean-like teeth and posterior Mytilacean-like teeth, since the anterior teeth or corrugations of *Ostrea edulis* are not described as present in *Ostrea* spp. or *Pinna* spp. by Bernard.

In *Ostrea edulis* (Linné) the two valves fit in a pill-box fashion as described for *Glycymeris*, the underlapping rim being very narrow. No specimens have been obtained by the recorder; material for the observation of the hinge being kindly provided by Dr. R. H. Millar. The larva has been described by Erdmann (1935).

According to Bernard (1898) three species of *Pinna* have triangular larvae. It can therefore be assumed that the larva of *Pinna fragilis* Pennant has a triangular shape and this, together with its hinge, should make it easily recognizable.

## ORDER EULAMELLIBRANCHIATA.

### Suborder HETERODONTA.

#### Superfamily Astartacea.

The larva shown on Plate II cannot be fitted into any other group. Its shape, texture and strength of the hinge are certainly reminiscent of *Astarte*. The inside view of the hinge, which must be regarded as incompletely observed, is shown in Text-fig. 3. It should be noted that the only hinge structure given is of a large, heavy larva (340 $\mu$ ).

The shell of the single specimen was tough and pinkish in colour with well-marked concentric lines.

According to Thorson (1936), larvae of *Astarte borealis* (Chemn.), *A. montagui* (Dillwyn) and *A. elliptica* (Brown) are non-pelagic. It is possible that our specimen is not a truly pelagic form but has been washed up from the bottom. Spat forms of other groups have occasionally been found in our collections.

#### Superfamily Cyprinacea.

A larva believed to be that of *Cyprina islandica* (Linné) is shown on Plate II. This is not the same larva as that indirectly identified as such by Jørgensen (1946), and it is suspected, from the incomplete description, that his larva is, in fact, a *Cardium* species.

*Cyprina islandica* (Linné) (+).—This larva may easily be mistaken for one of the Cardiaceae. It is, however, rather a flat larva and the hinge is different, but careful observation is required to distinguish the two types. The hinge resembles that of the Lucinacea and Erycinacea in having both the lateral teeth lamellar, and it is due to this resemblance that the larva has been identified as *Cyprina*.

## Superfamily Lucinacea.

Too little material of this superfamily has been obtained to allow a complete definition of the hinge. However, the definition of the hinge at  $300\mu$  (p. 84) should be sufficient for identification, if not to throw light on the taxonomic relationships.

The texture of prodissoconch I assists recognition of the larvae of the Lucinacea and Erycinacea since there are only radial streaks towards the margin. In all other groups of the Eulamellibranchiata (with the possible exception of the Astartacea where the texture is unknown) the prodissoconch I is evenly granulated all over.

Two species are shown on Plate I.

*Myrtea spinifera* (Montagu) (+).—The identification of this and the following species has been based on the shape of the prodissoconch of small shells.

The shell is colourless. The concentric lines are very fine towards the umbo but getting more strongly marked towards the edge and not so closely set.

*Phacoides borealis* (Linné) (1).—The shell is very similar in shape to *Montacuta ferruginosa* larva, but easily distinguished from that species by the well marked concentric lines.

Of the three or four other species listed as occurring in the North Sea proper, *Thyasira flexuosa* (Montagu) is known to be non-pelagic (Thorson, 1936).

## Superfamily Erycinacea.

[For references see Jørgensen (1946): in addition Sullivan (1948) has described *Rochefortia planula* Stimpson.]

Most, if not all, of the species of this superfamily are incubatory in the earlier larval stages. It is probably a good rule in this group that the shape of the larva is reminiscent of the adult. Five species are shown in Plate II. The hinge was described on p. 84. For the texture of prodissoconch I see under Lucinacea.

*Mysella bidentata* (Montagu) and *Montacuta substriata* (Montagu) (++).—*M. bidentata* has been described by Jørgensen (1946).

These two species are considered together because it is not known how they may be separated in the smaller pelagic stages. The difference in shape even at  $500\mu$  is not considerable (Plate II). Both have somewhat flat shells which are colourless, with faint, close-set concentric lines, though in later stages the shell may be slightly yellow and the concentric lines a little stronger.

These are the largest larvae that have been obtained in the recorder collections, specimens over  $500\mu$  being not uncommon. One specimen of *M. bidentata*, in which the dissoconch had begun to form, had a prodissoconch measuring  $635\mu$ .

*Montacuta ferruginosa* (Montagu) (++).—This has been described by Jørgensen (1946). Larvae greater than  $400\mu$  have not been seen.

*Kellia suborbicularis* (Montagu) (+).—This has been described by Lebour (1938a). Smaller stages than those illustrated in Plate II are more truly circular and symmetrical. The shell is colourless with fine concentric lines with slightly stronger concentric lines at frequent intervals.

SPECIES A. (? *Lepton squamosum* (Montagu)) (+).—The concentric lines are faint but widely set.

The only other species listed by Haas as occurring in the North Sea, apart from those recorded only in the coastal areas, are *Lasaea rubra* (Montagu) and *Turtonia minuta* (Fabricius)<sup>1</sup>. *Lasaea rubra* larvae are retained in the parental gill pouch until they have the adult form (Lebour, 1938b).

<sup>1</sup> Thiele (1935) places *Turtonia* in the Cyamacea but expresses uncertainty.



## Superfamily Cardiacea.

[For references see Jørgensen (1946): in addition Sullivan (1948) has described *Cardium pinnatulum* Conrad.]

The larvae of this superfamily may have high umbones, as in *Cardium ovale* Sowerby (Jørgensen, 1946) and *C. pinnatulum* (Sullivan, 1948), or low umbones as in *C. edulis* Linné (Jørgensen, 1946 and Lebour, 1938), *Cardium* spp. (Odhner, 1914) and Forma  $\mu$  (Borisjak, 1909). Some are very convex as in *C. echinatum* L. (Lebour, 1938) or not convex as in *C. crassum* Gmelin, *C. scabrum* Philippi and *C. edulis* (all three in Lebour, 1938). In spite of these apparently large differences the larvae of the Cardiacea conform to a basic type. Five species are shown in Plate II and the resemblance between them is clear, though *Cardium* A (*C. ovale*) is high-umboned and the other four low-umboned, and *Cardium* D and E very convex and *Cardium* A, B and C not convex. The resemblance is enhanced by the rather distinct pallial line which is set well away from the shell margin. The hinges of the high-umboned and low-umboned types are shown in Text-fig. 3.

*Cardium* A (? *C. ovale* Sowerby) (++).—This larva has relatively high umbones and is fairly convex, but by no means as convex as some other *Cardium* species. Larvae as large as 340 $\mu$  have been obtained.

*Cardium* B (++).—This is the least convex of the five larvae. The concentric lines are quite distinct but closely set. The largest larvae seen were 260 $\mu$ .

*Cardium* C (1).—This resembles *Cardium* B in convexity and texture.

*Cardium* D (++).—This is a very convex larva. Texture resembles *Cardium* B.

*Cardium* E (1).—This resembles *Cardium* D in convexity and texture.

Of the eight North Sea species of *Cardium*, five have already been described by Jørgensen (1946) and Lebour (1938) so that at least two of the above have been previously described. There has been, however, little success in assigning the above larvae to species from these descriptions. *Cardium* A agrees quite closely with Jørgensen's description of *C. ovale* (as *fasciatum*). It is certain that *C. edule* and *C. scabrum* are not included in them and probably not *C. crassum*. The convexity of the larvae and their frequency suggests that *Cardium* C is *C. minimum* Reeve, *Cardium* D is *C. echinatum* and *Cardium* E either *C. aculeatum* Linné or *C. exiguum* Gmelin.

## Superfamily Veneracea.

[For references see Jørgensen (1946); in addition Sullivan (1948) has described *Venus mercenaria* L., *Petricola pholadiformis* Lam., *Pitar morrhuana* Gould and *Gemma gemma* Totten.]

This is a difficult group since the larvae do not, as a rule, reach a large size and specific differences need to be recognized at a size of 200 $\mu$  to 250 $\mu$ .

Eight species are shown on Plate III and the difficulty of separating these eight is apparent from the photographs. The hinges do not greatly help since seven of them have Type *c* hinges (Text-fig. 3) and only VENERID G has Type *a*. In practice texture is a valuable aid but, unfortunately, is not adequately illustrated. Nevertheless, the seven species with Type *c* hinges are divided into four groups according to texture.

- (a) Concentric lines well marked and well separated (VENERIDS A and B).
- (b) Concentric lines moderately marked and moderately set (VENERID C).
- (c) Concentric lines moderately marked but close set (VENERIDS D and F).
- (d) Concentric lines fine and close set (VENERID E and *Petricola*).

The shells of Venerid larva have a light flaxen colour. The lateral ridges are very distinct, the posterior one extending about half-way round to the ventral side and the anterior about one-third of the way round.

VENERID A (? *Venus ovata* (Pennant)) and VENERID B (? *Venus striatula* (da Costa)) (+++).—

The hinges and texture of these two larvae are identical. In some specimens the concentric lines are well marked and well separated right up to prodissoconch I; in others the lines become less marked and closer set towards the prodissoconch. These two types, however, appear in both species and such a difference cannot be used to delimit species.

In order to distinguish the two larvae the only suitable feature is the shape of the dorso-lateral edge of the narrow end. In VENERID A this is nearly straight whilst in VENERID B it is convex. In the former too, the narrow end is rather more ventral than in VENERID B.

Jørgensen (1946) has described larvae which may be either *V. striatula* or *V. ovata* or a mixture of both.

VENERID (? *Venus*) C (+).—The curvature of the dorsal part of the narrow end is greater than in VENERID B and the larva is almost equilateral. Texture immediately distinguishes this larva from VENERIDS A and B.

VENERID (? *Venus*) D (+).—The dorso-lateral part is not so curved as in VENERID C. The 290 $\mu$  specimen, though exceptionally large for North Sea Venerids, had a hinge no different from the Type *c* hinge of much smaller specimens (<200 $\mu$ ). An interesting feature was a break in the dorso-lateral edge of the narrow end, marking off a lunule towards the umbo, from the main body.

VENERIDS (? *Dosinia*) E and F (+).—It is noticeable that, in the four species just described, the broad end falls away immediately from the umbo, and it can hardly be said that there is a dorsal edge. In these two larvae a dorsal edge is recognizable (left-hand side of photographs). In VENERID E this dorsal edge is more obtuse to the hinge line, in comparison with VENERID F, and the pointed part of the narrow end is situated more towards the dorsal side. Texture, too, distinguishes the two forms, but not very definitely.

VENERID (? *Paphia*) G (++).—This is readily distinguished from the other species described by the Type *a* hinge. The concentric lines are moderately marked, and moderately set towards the rim and fine and close set towards the umbo. A specimen in which the dissoconch had begun to form had a prodissoconch of 240 $\mu$ .

*Petricola pholadiformis* Lamarck (1).—This has been identified by Sullivan's (1948) description. It has a firmer shell than is usual in the larvae of the Veneracea and is more strongly coloured. As to be expected with a heavy shell, the main provincular projection is relatively strong.

From the distribution of the larvae and the shape of the prodissoconchs of bottom-living stages there is little doubt that VENERIDS A and B are *V. ovata* and *V. striatula* (or vice versa). The basic shape and hinge of the genus *Venus* are thus indicated so that VENERIDS C and D also seem to be *Venus* species though *Mysia undata* (Pennant) must also be considered as a possibility. The basic shape for VENERIDS E and F is different though not markedly so, and they are therefore considered to be the two species of *Dosinia*. VENERID G is thought to be a *Paphia* species since its hinge is unlike those of the suggested *Venus* and *Dosinia*. Furthermore, Miyazaki (1936) described the larva of *Paphia philliparum* as having a "taxodont" hinge and Dr. Quayle has told me that *Paphia* sp. investigated by him at Millport had a Type *a* provinculum. From the appearance of the prodissoconch of the bottom stages it is unlikely that the larva of *Garfarium minimum* (Montagu) is represented in the above.

### Superfamily Mactracea.

[For references see Jørgensen (1946); in addition Sullivan (1948) has described *Spisula solidissima* (Dillwyn) and *Mulinia lateralis* Say].

There is more disagreement about specific boundaries in this group than in any other, and it is perhaps hardly surprising that the larvae of more species have been proposed here than are listed by Haas (1926).

The two types of hinges are described on p. 85 and shown in Text-fig. 3. Six species are shown in Plate III and of these all except *Mactra corallina* (?) have the Type *a* hinge. It



is desirable here to add to the general description of the Type *a* hinge given above. Of the rectangular teeth that constitute the provinculum one, in particular, is prominent. This is on the posterior of the right valve. There is a tendency for the other teeth to be suppressed, making this tooth even more prominent, the amount of suppression being greater in some species than others. In *S. elliptica* (?) there is little and consequently this posterior right tooth is by no means so prominent. In *S. subtruncata* (?), *S. solida* (?) and *Lutraria lutraria* (?) there is a variable but good degree of suppression and the tooth is very prominent. In MACTRID E the suppression is midway between *S. elliptica* (?) and the others.

The prominent tooth makes it possible to place a larva in the Mactracea at a size (150 $\mu$ ) which otherwise would be too small for certainty. The species of these larvae have been determined chiefly on the basis of their distribution and there is not much doubt as to the species of MACTRIDS A-D.

MACTRID A (? *Mactra corallina* (Montagu)) (++).—The Type *c* hinge immediately separates this species from the other five. In shape it is easily recognized due to the very low umbones and the truncated broad end. The shell is yellowish along the ventral side and the concentric lines are very fine and close set with two or three stronger lines at wide intervals.

MACTRID B (? *Spisula solida* (Linné)) (+).—This is easily recognized by the very well-marked, well-separated concentric lines. The shell has a characteristic rich brown colour due to a chitinous covering of the same type as found in some adult shells of the species. A specimen measuring 360 $\mu$  has been obtained. The texture allows identification of this species at 170 $\mu$ , possibly earlier.

MACTRID C (? *Spisula subtruncata* (da Costa)) (++).—This has been described by Kändler (1926) and Jørgensen (1946) but in neither case is the description adequate.

There is a distinct dorsal shoulder to the broad end. The smaller larvae are narrower than the other Mactrid larvae of the same length.

The shell has two textures, a surface texture of fine, close-set concentric lines and a deeper texture of concentric markings widely separated. This deeper texture gives the impression of being a much reduced form of texture found in *S. solida* (?). The shell is yellowish and in most, but not all, specimens there is a tinge of rose colour at the narrow end.

MACTRID D (? *Spisula elliptica* (Brown)) (+++).—The truncated broad end and the high umbones are characteristic, the truncation being very clear in the bivalve condition. The concentric lines are fine, tending to group in bands. The shell is yellowish and the larger larvae have rather fragile shells. The largest measured was 355 $\mu$ .

MACTRID E (++).—The intact larva was at first mistaken for *M. corallina* (?) which it resembles in shape and texture. The umbo is, however, rather higher and the narrow end is round, rounder than in the other Mactrids and consequently it is more equi-valve than the others. The texture is rather firmer than in *M. corallina* (?) and the concentric lines, though close set, are very distinct. The mactrid tooth appears later; there is no sign of it at 290 $\mu$ .

MACTRID F (? *Lutraria lutraria* (Linné)) (++).—The hinge of this larva is very similar to *S. subtruncata* (?) and *S. solida* (?) but it is, nevertheless, difficult to assign it to any species other than *L. lutraria*.

Specimens, believed to be of this species, over 400 $\mu$  in size have been found in the recorder material. In these a part (an arc of ca. 20°) of the ventral edges of the two valves curled outwards, leaving a gap when the valves were closed.

There is one more Mactrid larvae than the distribution list of adults will allow. It is much more likely that this extra larva (which we believe to be MACTRID E) is of a species which has been taken to be merely a variety than that it is of a species still to be discovered in the North Sea. The possibility arises that it is the larva of *S. truncata* Montagu and that *S. truncata* is a true species and not simply a variety of *S. solida*. It may be pointed out that many workers have also taken *S. elliptica* to be a variety of *S. solida* (e.g. Jeffreys, 1863) though recent lists give them as distinct species.



## Superfamily Tellinacea.

[For references see Jørgensen (1946); in addition Sullivan (1948) has described *Tellina tenera* Say, *Macoma balthica* (L.) and *Cumingia tellinoides* Conrad.]

The basic shape of the larvae of this superfamily is similar to that of the adults. The species of *Tellina* can be distinguished from those of *Abra* by the fact that in the latter the umbones are higher and there is a distinct junction at the meeting of the umbonal sides and the body sides.

This distinction breaks down with the larva of *Tellina tenera* (Sullivan, 1948) which is of the *Abra* type. *Macoma balthica* (Sullivan, 1948), which is also a member of the Tellinidae has, however, the *Tellina* form.

The hinge and its development is described on p. 85 and shown in Text-fig. 3. The sizes placed against the stages in the figure are only a very approximate guide since there is considerable variation. It is possible that the hinges differ in the position of the ligament, the ligament being central, or nearly so, in *Tellina*, between the centre and the anterior end of the provinculum in *Abra* and at the anterior end in *Donax vittatus* (?). It cannot yet be said, however, that this is a definite rule.

Nine species are shown on Plate IV.

*Tellina fabula* Gmelin (++).—This may be recognized by the slight concavity of part of the dorsal edge of the broad, anterior end. The shell is almost colourless with moderately marked, moderately spaced concentric lines and a distinct pallial line. The larva has been identified by its distribution as in the case of the next larva.

*Tellina* A (? *T. pygmaea* Loven) (+).—This may be recognized by the angular character of the narrow posterior end. The shell is fairly firm and lightly coloured. The pallial line is distinct.

*Tellina* B (? *Tellina crassa* Pennant) (+).—In the larger specimen shown in Plate IV the dissoconch has begun to form. The larva is readily distinguished by the well-marked concentric lines on the prodissoconch; on the dissoconch the concentric lines are even more widely separated. Of the North Sea species of *Tellina* only *T. crassa* has strong concentric lines, the other species having fine lines.

*Tellina* C (1).—This is, presumably, either *T. squalida* (Pult.) or *T. donacina* L.

*Abra prismatica* (Montagu) (+++).—The *Abra* species are more easily identifiable in the bivalve state than in the single valve. This larva has very faint concentric lines between somewhat stronger lines placed at frequent intervals.

*Abra nitida* (Müller) (++).—The outline of this larva is more curved than that of *A. prismatica*. The narrow end is relatively longer. The concentric lines are very faint and the sculpturing is less than in the previous larva.

*Abra alba* (Wood) (+).—The broad end is much broader than in the two previous larvae. The concentric lines are very faint and somewhat irregular.

SPECIES A (? *Gari fervensis* (Gmelin)) (1).—This curious larva has an interesting resemblance in outline to the larva of *Cumingia tellinoides* (Sullivan, 1948).

It is distinctly inequivalve, the right valve being more convex than the left. The side views of both valves are shown in Plate IV, and it will be seen that there is a difference, too, in the concavities on both sides of the umbo, those on the right valve being more pronounced. The shell is fragile and colourless.

An inequivalve larva does not necessarily result in an inequivalve adult (see Solenacea) but such is to be expected unless there is other evidence. Amongst the Tellinacea only *Abra longicallus* (Scacchi) and *Gari fervensis* are distinctly inequivalve and in the former it is the left valve which is the more convex, in the latter the right valve. It is therefore likely that this larva is of *Gari fervensis*.

Jørgensen (1946) suggests, on the basis of egg size, that *Gari* (= *Psammobia*) *fervensis*

has non-pelagic larvae. This may be true and the single specimen found in the recorder material may have been washed up from the bottom. In fact, if *G. fervensis* has pelagic larvae, many more specimens should have been found in the material.

SPECIES B (? *Donax vittatus* (da Costa)) (+).—The texture of this shell is firmer than that of the three species of *Abra* described above. The shell is yellow-brown and usually with rose-red at the narrow end.

Of the remaining species of Tellinacea there should be no difficulty in identifying *Macoma balthica* from the information given by Werner (1939) and Sullivan (1948). *Macoma calcarea* (Chemn.) is non-pelagic (Thorson, 1936).

## Suborder ADAPEDONTA.

### Superfamily Solenacea.

[For references see Jørgensen (1946); in addition Sullivan (1948) has described *Ensis directus* (Conrad).]

It is considered that the description by Werner (1939) of *Cultellus pellucidus* really is of *Ensis ensis*. There is an easily recognizable difference between the hinge of *Cultellus* on the one hand and that of *Ensis ensis* and *Ensis siliqua* on the other, the hinge of the former being relatively shorter and stronger than in *Ensis*. The *Cultellus* hinge is shown in Text-fig. 3 and may be compared with that given by Werner which is now regarded as the *Ensis* hinge.

A distinctive feature for the group is the external ligament. In *Ensis* this begins to appear about 280 $\mu$  and becomes prominent with increasing size. It is shown in Sullivan's photograph of *E. directus*. (This feature in *Ensis* was pointed out to me by Dr. Quayle.) It is not a good diagnostic for *Cultellus* since it appears only in some very large specimens (>350 $\mu$ ) and even then is not prominent.

It is a curious fact that the three species to be described are inequivalve, the umbo of the right valve being higher than that of the left. This has not been noticed by previous authors, but it is not unimportant since a failure to recognize this feature leads to some confusion in separating small *Cultellus* and *Ensis siliqua*.

Three species are shown on Plate IV.

*Cultellus pellucidus* (Pennant) (+++).—Described by Jørgensen (1946) and others. The narrow end is pointed and is, or is nearly, upturned. The umbones are pronounced, though that of the left valve is distinctly lower. A larva of 400 $\mu$  has been seen but this is an exception.

The hinge teeth are present in larvae of 140 $\mu$ , or possibly less, in length.

*Ensis siliqua* (L.) (+).—Described by Lebour (1938). This is not so narrow as *Cultellus* and the posterior end is not so pointed and upturned. The height of the umbones is intermediate between *Cultellus* and *E. ensis*, the right umbo being comparable in height to the left umbo of *Cultellus*.

*Ensis ensis* (L.) (++).—This is readily distinguished by shape from the other two species. The posterior broad end is shorter and truncated and the larva is broader. The umbones are both low, with the left the lowest. This species is recognizable at 160 $\mu$ , possibly earlier.

*Solen marginatus* Montagu has not been recognized but the only North Sea records of the species are from the Continental west coast.

### Superfamily Saxicavacea and Family Myidae.

[For references see Jørgensen (1946); in addition Sullivan (1948) has re-described *Mya arenaria* L.] The hinge structure is shown in Text-fig. 3 and the valves in Plate V.

*Mya truncata* Linné (+).—This has been described by Jørgensen (1946) as having no hinge differentiation apart from the ligament. The accuracy of this, however, is to be doubted.



The shape agrees with the details given by Jørgensen, particularly in that the umbones are low. In components the hinge is identical with that of *Hiatella*, but the provinculum is thinner and the teeth much less pronounced. This identity extends even to the alternating lateral flanges.

The shell is slightly yellowish round the rim, and thin in comparison with *Hiatella*. The pallial line is comparatively indistinct.

There should be no difficulty in identifying *M. arenaria* from Sullivan's photographs and the hinge structure.

*Hiatella arctica* (Linné) (+++).—Described by Jørgensen (1946). Sullivan's (1948) description of *H. arctica* actually applies to *H. gallicana* but *gallicana* and *arctica* are sometimes taken to be merely varieties of one species, e.g. by Johnson (1934) whose nomenclature Sullivan has adopted.

This has a tough shell with a firm pallial line which is very noticeable even in intact bivalves. The shells have a yellowish colour round the rim, the concentric lines becoming better marked and more widely spaced away from the apex. The largest measured was 380 $\mu$ .

*Hiatella gallicana* (Lamarck) (++).—Described by Jørgensen (1946) and by Sullivan (1948) as *S. arctica*.

This is a rounder larva than *H. arctica* and the shell is thinner.

SPECIES A (? *Panomya arctica* Lamarck) (1).—In texture the strong shell is very similar to that of *H. arctica* but with a deeper colour. The pallial line is prominent.

SPECIES B (+).—The shell is fairly strong with moderately marked, moderately set concentric lines towards the margins. The shell is slightly yellow outside the fairly well-marked pallial line.

SPECIES C (1).—The shell is fairly strong with concentric lines fine and close set towards the umbo and more widely spaced towards the rim (230 $\mu$ ). The shell is yellowish outside the well-marked pallial line.

From Sullivan's (1948) photographs it can be said that *Mya arenaria* is not included in SPECIES A–C; neither can we fit any one of them to *Saxicavella jeffreysi* Winckworth as described by Jørgensen (1946, p. 303), but this identification is not certain. According to Haas' list there remain the following species in the North Sea: *Sphenia binghami* Turton (English coast only) and *Panomya arctica*. One must allow, however, for a further possibility in *Hiatella pholadis* (Linné) which is not accepted as a species by Haas (1926), is given as a doubtful one by Winckworth (1932) and accepted by Dautzenberg and Fischer (1912).

It is suggested that SPECIES A is *Panomya* on the basis of its texture. SPECIES B has been found chiefly off the Aberdeenshire coast which, following the distribution given by Haas, eliminates *Sphenia*. There is an impressive resemblance between the shapes of *H. arctica*, *H. rugosa* and SPECIES B, with *H. rugosa* forming the central type. While one cannot, of course, press the point, the interesting possibility that SPECIES B is *Hiatella pholadis* cannot be overlooked.

The identification of SPECIES C must remain unsuggested. Were it not for Jørgensen's (1946) drawing it would have been suggested that it is the larva of *Saxicavella jeffreysi*.

## Family Aloididae.

*Aloidis gibba* (Olivi) (+).—This has been indirectly identified by Jørgensen (1946), but his drawing bears little resemblance to the photograph on Plate V and much resemblance to some of the *Cardium* spp. (Plate II). The shape of our larva so clearly recalls that of the adult that it is very unlikely that the present identification is incorrect.

It is inequivalve, the umbonal region being more pronounced in the right valve (from about 150 $\mu$ ) and is very convex, almost as convex as it is broad.



The inside view of the hinge at  $250\mu$  is shown in Text-fig. 3. The dorsal view has, unfortunately, been obtained only for larvae no larger than  $190\mu$ .

The concentric lines and the pallial line are well marked.

The resemblance between this larva and the adult *Aloidis* is so marked that it may seem surprising that Jørgensen selected another larva as being this species. However, Boysen Jensen (1919) found that *Aloidis gibba* breeds (or a new brood appears in the bottom fauna) very seldom, and it is therefore possible that, though the adult is fairly common in the Sound, no larvae appeared in Jørgensen's collections during the period of his investigations.

### Superfamily Adesmacea.

#### Family Pholadidae.

[For references see Jørgensen (1946); in addition Sullivan (1948) has described *Zirfaea crispata*]. Four species are illustrated in Plate V. The typical pholad hinge, which is recognizable at  $150\mu$ , possibly earlier, is shown in Text-fig. 3.

*Zirfaea crispata* (Linné) (+ +).—The larva is characterized above  $300\mu$  by a ventral notch, with teeth, discussed by Werner (1939). The larva becomes more convex with increasing size. The shell is yellowish, particularly round the rim. Concentric lines are moderately marked, close set, with somewhat stronger lines set at frequent intervals.

PHOLAD A (? *Pholas dactylus* (Linné)) (+ +).—This is not easy to separate from *Zirfaea* at sizes less than  $300\mu$ . It is, however, more truly round than *Zirfaea*. In *Zirfaea* the breadth is very slightly greater than the length whilst in this larva the length is slightly the greater. The texture is like *Zirfaea*.

PHOLAD B (? *Barnea candida* (L.)) (+).—This is a deep larva with distinctive shape. The shell is almost colourless. There are frequent well-marked concentric rings with finer rings in between. One larva measuring  $260\mu$  had a ventral notch as in *Zirfaea* but this may have been the result of unusually early development.

PHOLAD C (? *Xylophaga dorsalis* (Turton)) (+).—This is of the same type as PHOLAD B, but the corner on one side is more towards the centre of the breadth.

PHOLAD A resembles Kändler's (1926) *Pholad* spp. which he believed to be *Pholas dactylus* or *Zirfaea crispata*. Since the latter is now known it is likely that this species is *Pholas dactylus*. Jørgensen (1946) has described *Barnea candida* which is very similar to PHOLAD B. The prodissoconch on a young *X. dorsalis* has the type of shape to which PHOLAD B and PHOLAD C conform, and it is therefore believed that PHOLAD C is this species.

#### Family Teredinidae.

[See Jørgensen (1946); in addition Sullivan (1948) has described *T. navalis* L.]. A single species is shown in Plate V and the hinge in Text-fig. 3.

*Teredo* sp. (2).—This is a convex larva with opaque, brownish shell. The concentric lines are very distinct and well spaced. The larva is characterized by radial rays which are very distinct. Sullivan's photographs clearly show that this is not *Teredo navalis*. Jørgensen has described *T. megotara* (Hanley) and Lebour (1938) *T. norvegica* (Spengler). Neither, however, mention the radial rays. The only other North Sea species is *T. bipinnata* (Turton) from the English coast.

### ORDER ANOMALODESMATA.

#### Superfamily Pandoracea.

Three larvae with shapes sufficiently distinct to show that they belong to different genera have the same type of hinge structure. It seems probable, therefore, that they are representa-

tives of the Anatinacea; the hinges of every other superfamily in the North Sea with three or more genera have been described above. The three larvae are shown in Plate V and the hinge in Text-fig. 3 and described on p. 86.

(? *Thracia* sp.) (+).—The shell is colourless, the concentric lines and pallial line poorly marked. The larva is slightly inequivalve, the right umbo being the more pronounced.

(? *Cochlodesma praetenu* (Montagu)) (1).—This was identified to the genus by its resemblance to the prodissoconch of a young *C. praetenu*, which is the only North Sea species.

The concentric lines are fairly well marked and closely set. The provincular projection is rough and appears toothed on inside view.

(? *Lyonsia norvegica* (Gmelin)) (++).—This larva has a very fragile shell, a feature in keeping with the adult character of the suggested species. Larvae of 300 $\mu$  are slightly inequivalve, the right umbo being very slightly the more pronounced.

Corresponding to the fragility of the larva the hinge is weakly developed and the provincular projection of the right valve is very small, even at a size of 260 $\mu$ .

Sullivan (1948) gives a photograph of the spat of *Pandora gouldiana* (Dall) in which the prodissoconch shape is shown very clearly. This establishes the generic shape of *Pandora* larvae.

### Superfamily Poromyacea.

A larva which apparently belongs to this superfamily is shown on Plate V and the inside view of the hinge of a 300 $\mu$  larva in Text-fig. 3. The 300 $\mu$  larva has two or three well-marked concentric lines, the rest of the lines being faint. There is no further information.

### APPENDIX.

A short list is given below of the synonyms used by Winckworth (1932) and by Haas (1926).

| Winckworth.                            | Haas.                                    |
|----------------------------------------|------------------------------------------|
| <i>Musculus niger</i> (Gray)           | = <i>M. discrepans</i> (Leach).          |
| <i>Chlamys distorta</i> (da Costa)     | = <i>Hinnites pusio</i> (L.).            |
| <i>Astarte montagui</i> (Dillwyn)      | = <i>Astarte compressa</i> (Mont.).      |
| <i>Astarte elliptica</i> (Brown)       | = <i>Nicania banksii</i> (Leach).        |
| <i>Cyprina islandica</i> (Linné)       | = <i>Arctica islandica</i> (L.).         |
| <i>Myrtea spinifera</i> (Montagu)      | = <i>Lucina spinifera</i> (Mont.).       |
| <i>Phacoides borealis</i> (Linné)      | = <i>Lucina borealis</i> (L.).           |
| <i>Mysella bidentata</i> (Montagu)     | = <i>Montacuta bidentata</i> (Mont.).    |
| <i>Montacuta ferruginosa</i> (Montagu) | = <i>Tellinomya ferruginosa</i> (Mont.). |
| <i>Cardium ovale</i> Sowerby           | = <i>Cardium fasciatum</i> Mont.         |
| <i>Cardium crassum</i> Gmelin          | = <i>Cardium norvegicum</i> Spengl.      |
| <i>Cardium scabrum</i> Philippi        | = <i>Cardium nodosum</i> Turt.           |
| <i>Venus striatula</i> (da Costa)      | = <i>Venus gallina</i> (L.).             |
| <i>Mysia undata</i> (Pennant)          | = <i>Lucinopsis undata</i> (Penn.).      |
| <i>Gafrarium minimum</i> (Montagu)     | = <i>Gouldia minima</i> (Mont.).         |
| <i>Paphia Röding</i>                   | = <i>Tapes</i> Meg.                      |
| <i>Mactra corallina</i> Montagu        | = <i>Mactra stultorum</i> L.             |
| <i>Tellina pygmaea</i> Lovén           | = <i>Tellina pusilla</i> Phil.           |

| Winckworth.                             | Haas.                                 |
|-----------------------------------------|---------------------------------------|
| <i>Abra</i> Lamarck                     | = <i>Syndosmya</i> Recluz.            |
| <i>Gari fervensis</i> (Gmelin)          | = <i>Gari ferroensis</i> (Chemn.)     |
| <i>Solen marginatus</i> Montagu         | = <i>Solen vagina</i> L.              |
| <i>Hiatella</i> Bosc                    | = <i>Saxicava</i> Bellevue.           |
| <i>Hiatella gallicana</i> (Lamarck)     | = <i>Saxicava rugosa</i> (L.).        |
| <i>Panomya arctica</i> (Lamarck)        | = <i>Panomya norvegica</i> (Spengl.). |
| <i>Saxicavella jeffreysi</i> Winckworth | = <i>Saxicavella plicata</i> (Mont.). |
| <i>Aloidis gibba</i> (Oliv)             | = <i>Corbula gibba</i> (Oliv.).       |

## SUMMARY.

1. A method of identification of lamellibranch larvae, based entirely on the shells of larvae which have developed beyond the veliger or "D-shaped stage," is described.

2. The characters of use are shape, hinge and texture.

3. The shapes of allied species are variations of a shape characteristic for the group. Since two or more groups of allied species may have a similar basic shape a classification of larvae by shape only is not satisfactory.

4. All pelagic larvae above a certain size (150 $\mu$  or less) have a hinge. By reference to some simple components all hinges can be reduced to a limited number of basic types. Classification of larvae by hinges results in a classification closely parallel to a classification of adults.

5. Generalizing, a larva can be assigned to a superfamily by its hinge, to genus and species by its shape, and its texture can sometimes be used to aid identification to species.

6. Seventy-seven types of North Sea lamellibranch larvae are described.

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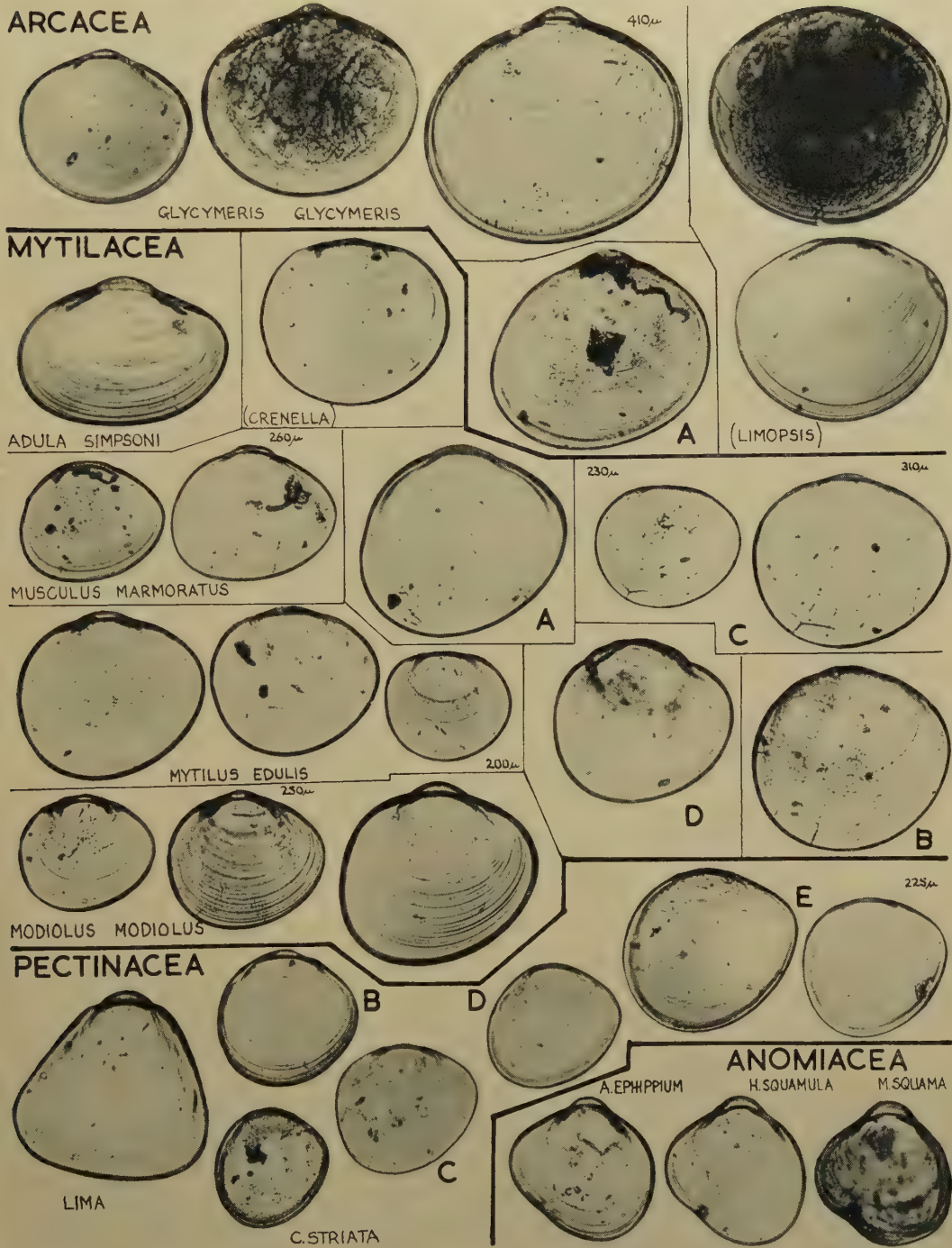
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#### EXPLANATION OF PLATES I-V.

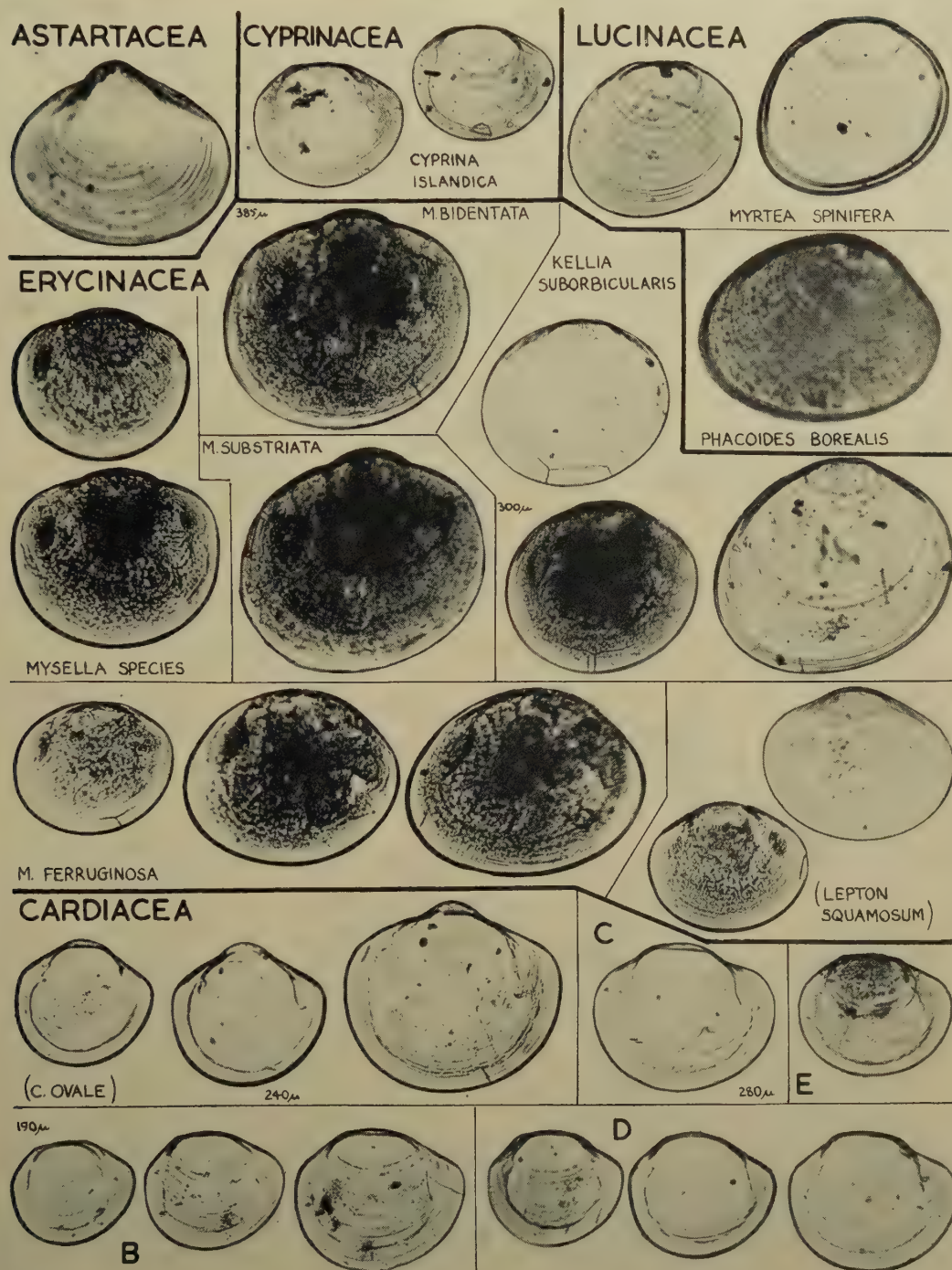
Photomicrographs of lamellibranch larvae grouped into superfamilies or families. The photographs are all equally enlarged ( $\times 90$ ) and the lengths of a few of the larvae are given on each plate. It should be noted that identifications in brackets are less certain than the others, as explained on p. 88.



Larvae of the Arcacea, Mytilacea, Pectinacea and Anomiacea.





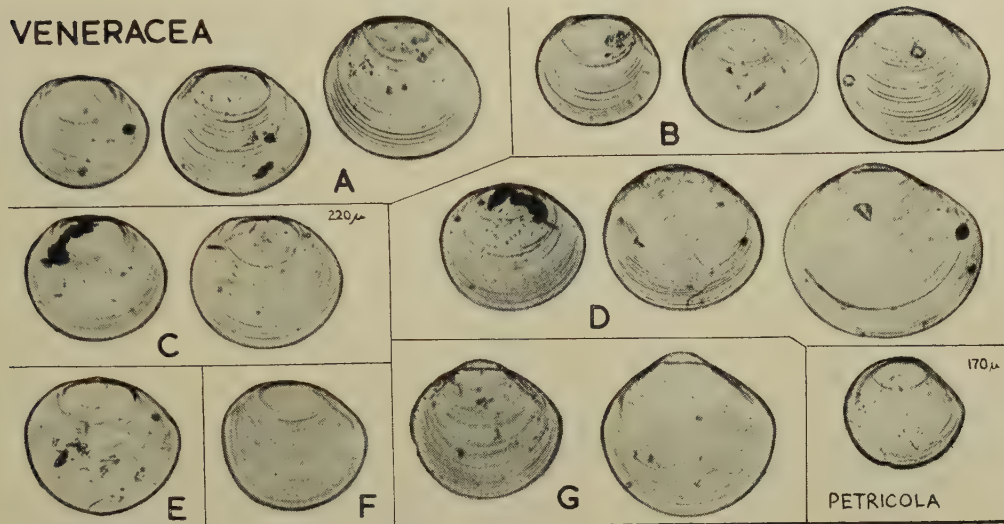


Larvae of the Astartacea, Cyprinacea, Lucinacea, Erycinacea and Cardiaceae.

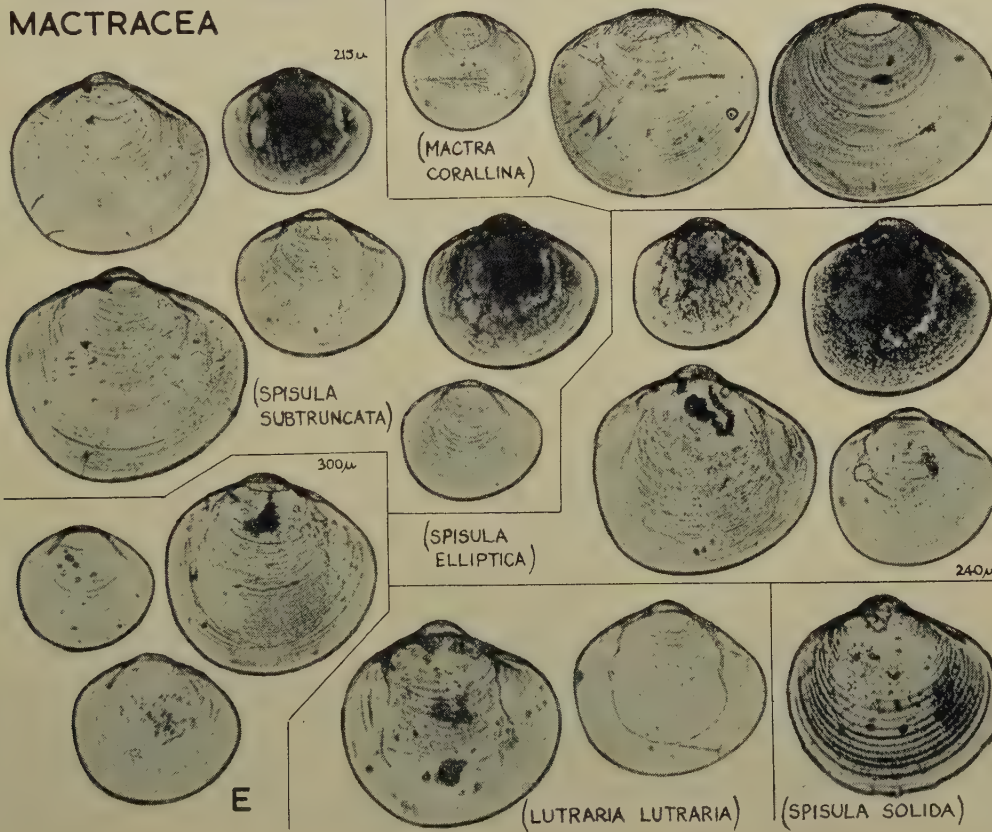




VENERACEA



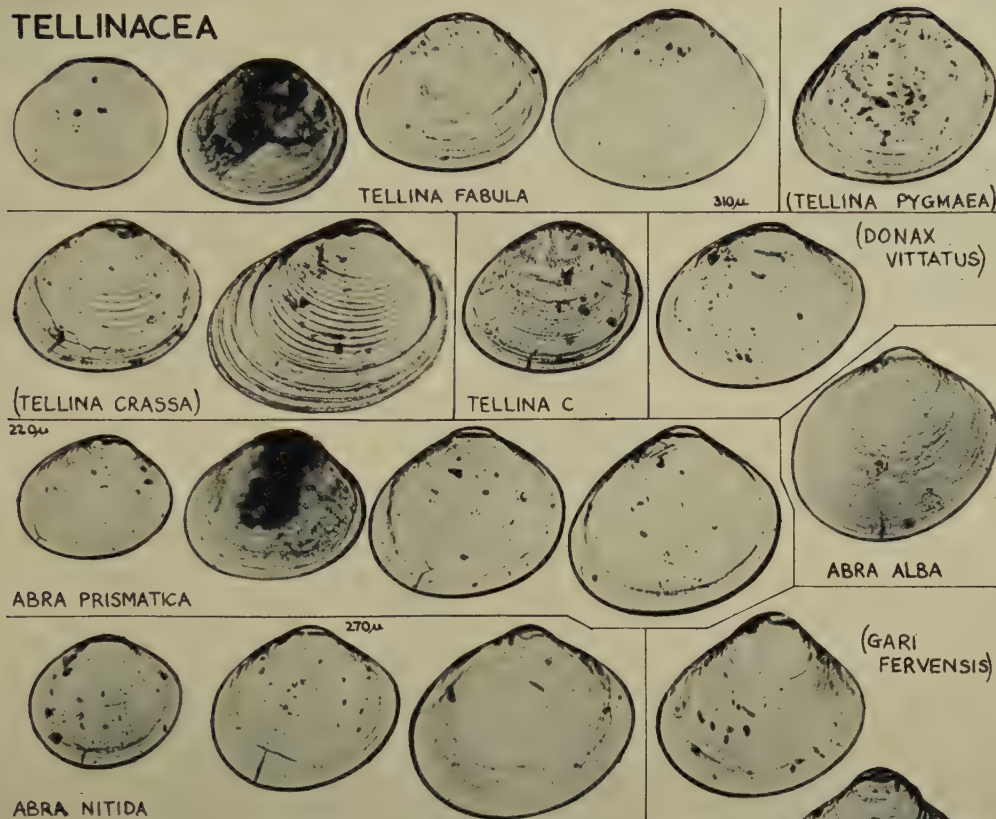
MACTRACEA



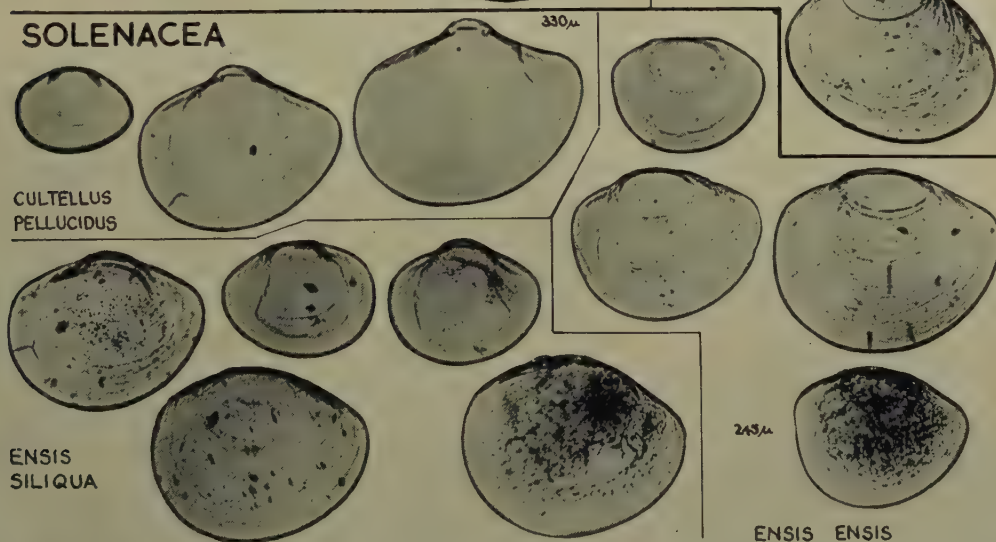
Larvae of the Veneracea and Mactracea.



TELLINACEA



SOLENACEA

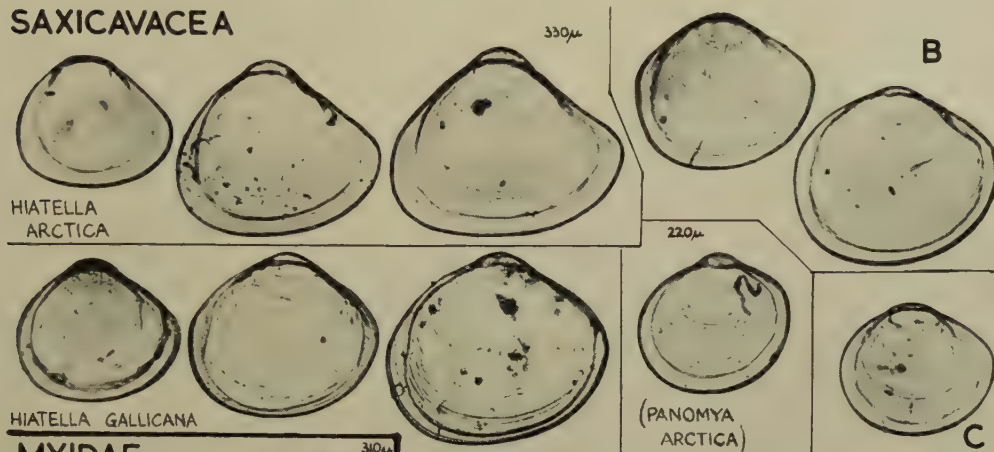


Larvae of the Tellinacea and Solenacea.

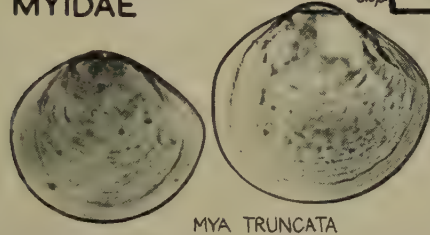




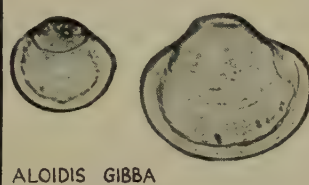
**SAXICAVACEA**



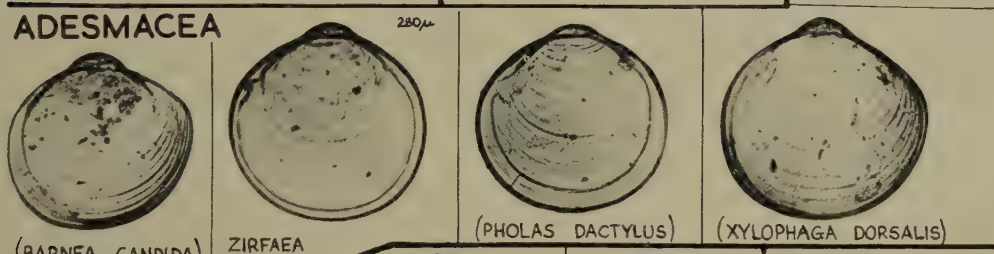
**MYIDAE**



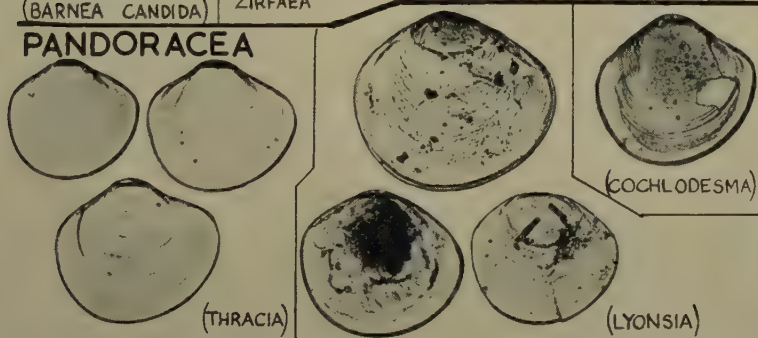
**ALOIDIDAE**



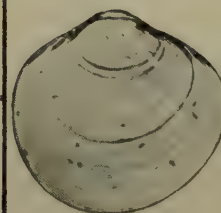
**ADESMACEA**



**PANDORACEA**



**PORO-MYACEA**



Larvae of the Saxicavacea, Myidae, Aloididae, Adesmacea, Pandoracea and Poromyacea.





CONTINUOUS PLANKTON  
RECORDS:  
FIRST REPORT ON THE DISTRIBUTION OF  
LAMELLIBRANCH LARVAE IN THE  
NORTH SEA

BY

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EDITORIAL NOTE.—It is thought that it may prove convenient for the reader to find this report on the distribution of the lamellibranch larvae next in the series to Mr. Rees' earlier account of his method of identifying the larvae. Consequently, to save repetition, it has been necessary for Mr. Rees to anticipate in his text the publication of the next 'Hull Bulletin,' No. 21, "Explanation and Methods, 1946-49."

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INTRODUCTION AND METHODS.

IN a recent Hull Bulletin (Rees, 1950) the lamellibranch larvae obtained by the Continuous Plankton Recorder in the North Sea were described and named specifically or otherwise labelled. These descriptions and identifications were the essential first stage in the study of the distribution of the larvae in the North Sea. It has long been recognized that knowledge of the areas and times of main spatfalls would have considerable economic advantages. Whilst, perhaps, the distribution of larvae alone might not show *positively* these areas, the grabbing and dredging for spat areas could be guided by the distributions and much time and labour saved. Another important matter is that it is essential to know the larval history of a bottom-living lamellibranch to understand its biology fully.

As explained in 'Bulletin' No. 21 (Rae, 1951), only the odd numbered 10-mile blocks (1, 3, 5, etc.) have been analysed during the *routine* plankton analysis in recent years. It has been more convenient to investigate the lamellibranch larvae

on the even numbered 10-mile blocks (2, 4, 6, etc.), and on these the proportions of the various species have been determined. This has been done more thoroughly than in initial or routine analysis, with the result that many more blocks have been found with larvae than without, which is the reverse to the finding during routine analysis. If, for example, there were only 10 larvae on a 10-mile block it is unlikely that one would be seen during routine analysis, and quite likely that some would be seen during the special analysis for lamellibranch larvae. The total numbers of larvae on these even blocks were not counted, but they were estimated by averaging the numbers found on the two adjacent odd numbered blocks for which counts were available. The number of larvae of each species on the even 10-mile blocks was then roughly estimated by splitting the total number according to the proportion of larvae of the various species. The quantitative estimate of the larvae is, consequently, indirect and quite approximate, but is adequate for the purposes of this report; our concern is with considerable differences in population density rather than with relatively minor ones.

A major difficulty has arisen from the fact that the silk in use is impregnated with an acid substance causing a fairly rapid deterioration of the larval shells in contact with the silk. Boiling the silk in water, the use of buffered formalin, and placing a bag of calcium carbonate in the tank of the Recorder have not entirely overcome this difficulty. Its effect has been minimized by analysing the larvae as soon as possible after arrival in the laboratory.

The distributions have been investigated thoroughly since August, 1948, but there is some scattered information prior to that. The 1949 distributions are chiefly used in this report, the earlier data being presented whenever it has appeared desirable.

#### DISTRIBUTION OF TOTAL LAMELLIBRANCH LARVAE.

In this section the results obtained during routine analysis are presented, irrespective of the specific content of the population.

The quantitative distribution of lamellibranch larvae in the southern North Sea during 1932-1937 is given by Henderson and Marshall (1944), and over the whole North Sea in 1938-39 by Marshall (1948). It is not proposed to publish similar maps for 1946-49. Instead, the distribution of blocks with more than 500 per 10 miles is shown in Text-fig. 1, using one symbol to cover the 1932-37 period, another for 1938-39 and others for each of the years 1946 to 1949.<sup>1</sup> As a result of the specific analysis of 1948 and 1949 some of the patches can be considered later in detail and, for ease of reference, these have been numbered in Text-fig. 1. In the meantime it should be stressed that in no year were all these patches found.

In Text-fig. 2 the distribution of blocks with over 1000 larvae per 10 miles is

<sup>1</sup> In recent years alternate 10-mile blocks only have been analysed. In preparing all the charts in this paper it has been assumed that if a certain distribution was found on alternate blocks the same distribution occurred on the unanalysed intermediate block, *e.g.*, if a certain symbol applies to blocks 5 and 7 on a line, the isolated symbols have been joined through block 6, though this latter block was not analysed. This procedure serves merely to simplify the visual appearance of a chart.

plotted. Many of the lesser patches of Text-fig. 1 have disappeared, but the patches east and northwards of the Dogger Bank remain distinctive.

When the Recorder samples along a standard route, the same 10 miles over the sea bottom is, theoretically, analysed for plankton time after time. In Text-fig. 3 graphs are shown of the average number of lamellibranch larvae obtained on each analysed 10-mile block throughout various years on some standard lines; the larvae obtained over the same 10 miles of sea bottom have been summed, divided by the number of observations, and plotted. The geographical positions of the various 10-mile blocks are given in 'Hull Bulletin' 7 (Hardy, 1941, Text-fig. 1). These graphs serve to illustrate the distribution of larvae in 1949 compared with that of 1938 or 1939. The Leith-Skagerrak line was off its standard route in June and July, 1938, and the standard routes from September, 1938, to August, 1939, have been used. Other graphs in this figure, relating to Recorder lines taken in 1938-39 only, are relevant to the discussion which follows.

An important feature of the distributions in Text-fig. 1 is the consistency in place of occurrence of high densities of larvae. This is more considerable than the visual appearance of the chart indicates, since two of the symbols serve for more than one year and, again, some areas were sampled for a few months only (in one month only in the case of one patch) during the whole period of the Recorder programme. For example, the east Dogger Bank patch (6) was recorded in 1934, 1935 and 1949; the Skagerrak patch (4) in 1938, 1939, 1948 and 1949. A striking instance of consistency is shown in Marshall's (1948) charts. Just south of the Dogger, on the Leith-Hamburg line, a patch 20 miles across was recorded in May and July, 1938, and again in July, 1939. On the Leith-Skagerrak line, too, the graphs for 1939 and 1949 (Text-fig. 3) are strikingly similar over the stretch running from 190 miles east of the Forth to the Skagerrak, a peak in numbers occurring 250 miles from the Forth in both years. In 1948, again, a similar peak occurred 250-270 miles from the Forth.

Another notable feature of the distribution is that, except for a small patch in 1946, high concentrations of larvae were not found over the main area of the Dogger Bank, despite the high adult population. The Hull-Copenhagen line is not quite satisfactory for determining conditions over the main Dogger Bank, since it runs rather towards the southern edge. In 1938 and 1939, however, there were two lines which crossed over the main Bank, the Hull-Norway and Leith-Hamburg lines (see Text-fig. 1 in Hardy, 1941). On these two lines the average number of the larvae found on each block throughout the year is shown in Text-fig. 3, the position of the Dogger Bank being indicated. These graphs show clearly the scarcity of larvae over the Dogger. During 1946 and 1947, before ships resumed their standard routes, many Recorder lines crossed the main Dogger but, apart from the slight patch in 1946, no concentrations were found. In 1947 the Hull-Copenhagen route passed 15-20 miles north of the standard route and provided a good series of lines passing over the main Dogger; the high numbers at the western end of the line ended abruptly at the edge of the Bank (Text-fig. 3).



Regarding the comparison of the years, attention may be directed to the very high numbers east of the Dogger Bank (Hull-Copenhagen) in 1949 and off the Humber in 1947, the high numbers off the Forth (Leith-Skagerrak) in 1949, and the scarcity of larvae on the Aberdeen-Lerwick line in 1949.

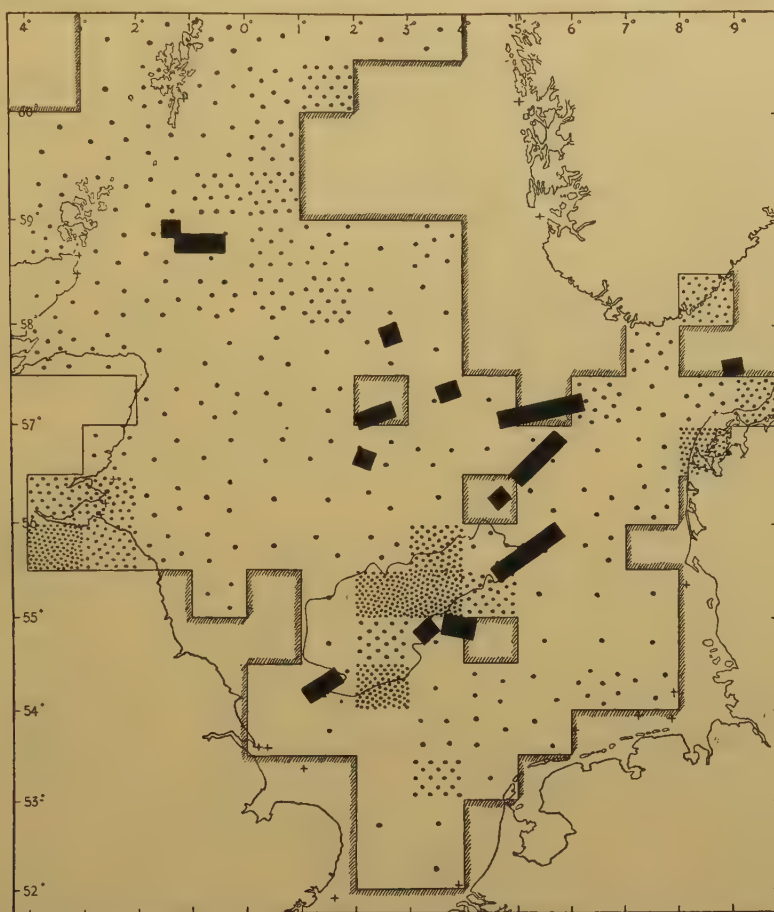
It would be of interest to compare the numbers of larvae obtained by the Recorder with other results. The highest number ever attained per 10-mile block



TEXT-FIG. 1.—Chart showing the distribution of 10-mile blocks with more than 500 lamelli-branch larvae during the periods 1932-37, 1938-39, and each year from 1946 to 1949. The Dogger Bank is shown. Some patches have been numbered for convenience of reference in the text.

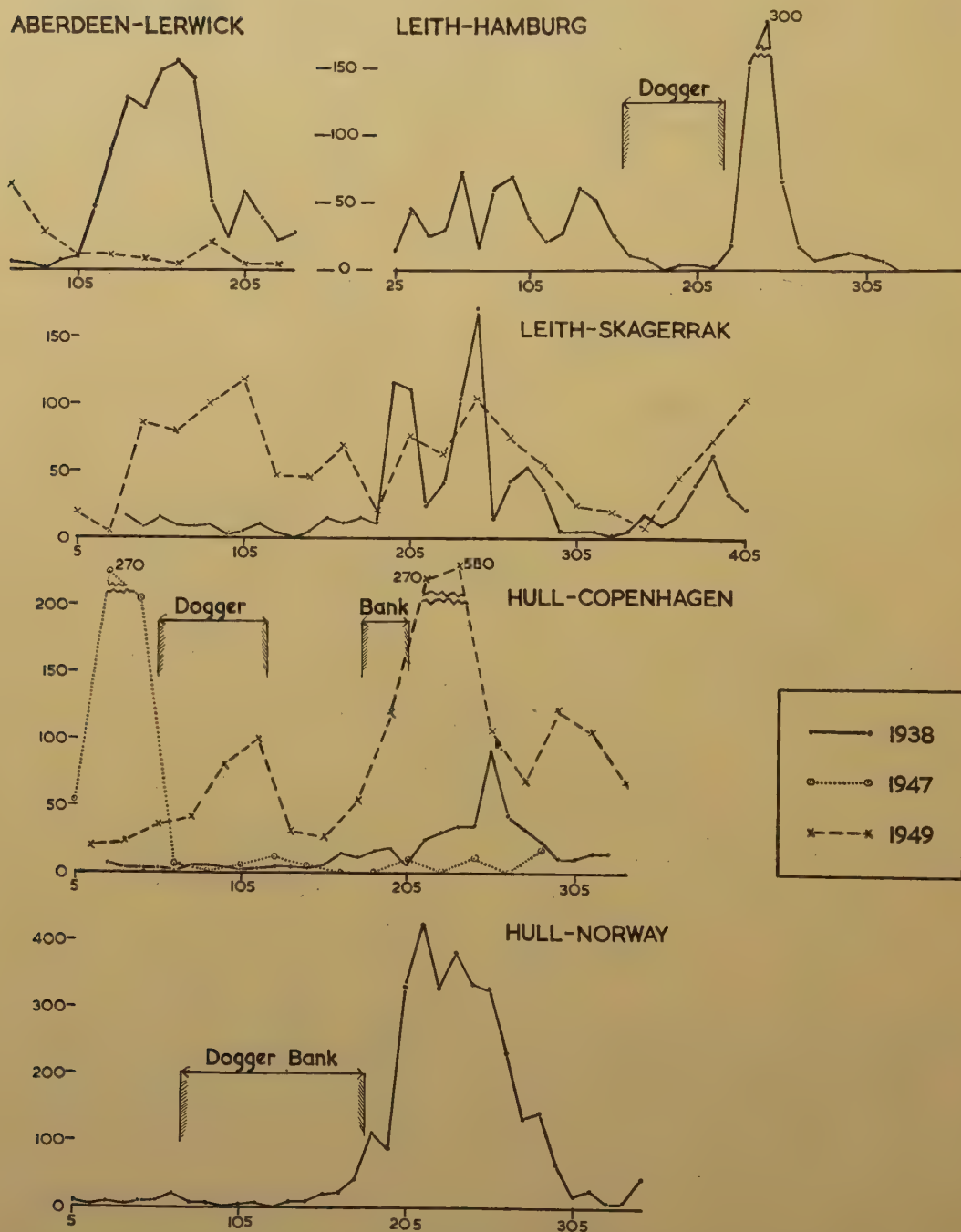
was estimated to be 9000. In passing through 10 miles the Recorder filters nearly 3 m<sup>3</sup> of water, thus giving the average density at 10 m through these 10 miles as 3000 per m<sup>3</sup>. It is certain that "smoothing" occurred and that the density over a shorter tow than 10 miles was higher. This value can be compared directly with those for larvae of *Ostrea edulis*. Gaarder and Spærek (1932) found 2000-6000 oyster larvae per m<sup>3</sup>. Korringa (1941) gives a few thousand at the height of the

season, with 10,000 or more during swarming. These productions are, however, conserved by two factors: (a) for the first 10 days or so *Ostrea edulis* larvae are incubatory and consequently early mortality must be lower than in fully pelagic larvae, (b) the hydrographic conditions were such as not to disperse the larvae. Thorson (1946) gives figures from pump collections. These pump collections probably contained a large proportion of "D-shaped larvae," whilst such small



TEXT-FIG. 2.—The black rectangles show the distribution of all 10-mile blocks, obtained during the entire Recorder survey, with more than 1000 lamellibranch larvae. The density of bottom adults is represented by dots, each dot standing for 5 adults (nearest) per  $m^2$  per international square (see p. 111). The hatched boundary line encloses squares not sampled during the quantitative surveys of the bottom fauna.

larvae rarely enter into the counts of larvae on recorder silk. Thorson's figures are thus probably heavily weighted in comparison with our results. Out of 74 individual pump hauls Thorson had 1 which exceeded 3000 per  $m^3$ , this being 3380 per  $m^3$ , of which 86% were not identified to species and were, presumably, at the D-shape stage.



TEXT-FIG. 3.—Graphs giving the average number of lamellibranch larvae obtained on each analysed 10-mile block throughout one year on some standard Recorder routes. The position of the 10-mile blocks can be seen by comparing the horizontal scale of miles with the chart in Text-fig. 1 of 'Hull Bulletin' 7. The Dogger Bank is indicated.



Marshall (1948) has charted the number of bottom-living lamellibranchs per m<sup>2</sup> for each international square of the North Sea as derived from Davis (1923, 1925) and Stephen (1933). Since this chart will be used later in this report some of the empty squares may be filled in by adding the results of Petersen (1914) off the Danish coast and mouth of the Skagerrak: 17 in L11, 46 in M14, 14 in M13, 20 in M12, 24 in M11 and 320 in N13. The international squares are shown in the key chart on Plate VIII.

#### DISTRIBUTION OF THE SPECIES.

The approximate quantitative distribution of larvae is shown in the series of maps in Plates VI–VIII. For one reason or another some of the larvae described by Rees (1950) are omitted. The same nomenclature is used as in the descriptive report, and attention should be drawn to the method used to indicate uncertain identifications, *e.g.* (? *Limopsis*).

The coverage of the North Sea month by month is a matter of much importance, and for proper consideration of the maps of distribution the coverage shown in Rae (1951) should be consulted. It depends on the particular species whether the absence of a certain line during a month is likely to be important or not. For example, the absence of a Leith-Skagerrak line in April and May is important in the case of a spring larva, such as *Ensis ensis*, but not in the case of an autumn form like *Montacuta ferruginosa*.

It was hoped to present in figures the known quantitative distribution of the relevant bottom-living species in the North Sea since, apart from the chart of all species combined given by Marshall (1948), the results are in tabular form. This would require, however, the publication of many more maps. Furthermore, only Davis (1923, 1925) and Petersen (1914) give full quantitative data, and it is possible that their results are now inapplicable to large stretches of the North Sea.

The alternative adopted is to show by means of a dot, on the maps of larvae (Plates VI–VIII), those international squares where the particular species were found by one or more of the four authors, Davis (1923, 1925), Stephen (1933), Petersen (1914) and Schrader (1911).<sup>1</sup> A key is given in Plate VIII showing the squares sampled by the four workers. It should be noted that Stephen (1933) gives only the more numerous or interesting species obtained by him. Some quantitative information on adults is given in the text, this, normally, being the highest density found by the authors referred to.

#### Seasonal Occurrence.

The seasonal distribution of the various species is presented in tabular form in Table I, the criterion being the number of blocks in each month of 1949 on which the species was found. The alternative of taking the total number of larvae of a species obtained in each month as the criterion has been rejected, since, by this

<sup>1</sup> A few adult occurrences have been omitted where it has been inconvenient to extend the area of a chart to include them. Mention is made in the text of omissions that appear to be important.

method, it is possible that an intense breeding of a dense, but local, adult population in one month would overshadow a more widespread breeding in another month. For the purpose of an overall picture a widespread breeding is of greater interest than a localized breeding. Species observed on less than 10 blocks throughout the year are not listed, but the season of occurrence of most of these can be read from the charts, which also give fuller information for the species included in the table. Thus, no particular month is marked out in the table for *Zirfaea crispata*, but the charts show that April and May were the peak months.

TABLE I.—The Number of 10-mile Blocks on which Larvae were Observed in Each Month of 1949.

|                                |    | J  | F | M | A | M | J | J | A | S | O | N | D |
|--------------------------------|----|----|---|---|---|---|---|---|---|---|---|---|---|
| (a)                            |    |    |   |   |   |   |   |   |   |   |   |   |   |
| <i>Ensis ensis</i> ..          | .. | .. | . | . | * | * | + | + | . | . | . | . | . |
| <i>Zirfaea crispata</i> ..     | .. | .. | + | + | + | + | + | . | . | . | + | + | + |
| (? <i>Lyonsia</i> ) ..         | .. | .. | . | + | + | + | + | . | . | . | . | . | . |
| (b)                            |    |    |   |   |   |   |   |   |   |   |   |   |   |
| " <i>Montacuta</i> " ..        | .. | .. | . | . | . | . | + | * | + | + | + | + | . |
| <i>Cardium</i> A ..            | .. | .. | . | . | . | . | + | + | . | + | + | . | . |
| <i>Hiatella gallicana</i> ..   | .. | .. | . | . | . | + | + | + | + | . | + | . | . |
| (c)                            |    |    |   |   |   |   |   |   |   |   |   |   |   |
| <i>Glycymeris glycymeris</i>   | .. | +  | . | + | . | . | + | + | + | ● | ● | ● | * |
| (? <i>Limopsis</i> ) ..        | .. | .. | . | . | . | . | . | . | . | + | + | + | . |
| <i>Adula simpsoni</i> ..       | .. | .. | . | . | . | . | . | . | . | + | + | + | . |
| <i>Modiolus modiolus</i> ..    | .. | .. | . | + | . | . | + | + | + | + | * | * | + |
| <i>Lima</i> ..                 | .. | .. | . | . | . | . | . | . | + | + | + | + | . |
| <i>Montacuta ferruginosa</i>   | .. | .. | . | . | . | . | . | + | + | ● | ■ | * | . |
| <i>Cardium</i> D ..            | .. | .. | . | . | . | . | . | . | . | + | + | + | . |
| Venerid A ..                   | .. | .. | . | . | . | . | . | . | . | * | * | . | . |
| Venerid B ..                   | .. | .. | . | . | . | . | . | . | . | . | + | + | . |
| (? <i>Paphia</i> ) ..          | .. | .. | . | . | . | . | . | . | . | + | + | + | + |
| <i>Abra prismatica</i> ..      | .. | .. | . | . | . | + | + | + | + | ● | ● | * | . |
| <i>Abra nitida</i> ..          | .. | .. | . | . | . | . | . | . | . | + | * | + | + |
| <i>Cultellus pellucidus</i> .. | .. | +  | + | + | + | + | + | + | + | * | ■ | * | + |
| <i>Hiatella arctica</i> ..     | .. | .. | . | . | . | . | + | + | + | + | * | * | + |
| (? <i>Pholas dactylus</i> ) .. | .. | .. | . | . | . | . | . | . | . | + | + | + | . |
| (d)                            |    |    |   |   |   |   |   |   |   |   |   |   |   |
| (? <i>Mactra corallina</i> )   | .. | +  | + | + | * | + | . | . | . | . | + | . | . |
| (? <i>Mactrid</i> E) ..        | .. | .. | . | . | * | + | . | . | . | . | . | + | . |
| (e)                            |    |    |   |   |   |   |   |   |   |   |   |   |   |
| <i>Mytilus edulis</i> ..       | .. | .. | . | . | . | + | * | * | + | + | + | * | + |
| <i>Cardium</i> B ..            | .. | .. | . | . | . | . | + | . | . | + | + | + | . |

|                                 |    |    | J  | F | M | A | M | J | J | A | S | O | N | D |
|---------------------------------|----|----|----|---|---|---|---|---|---|---|---|---|---|---|
| (f)                             |    |    |    |   |   |   |   |   |   |   |   |   |   |   |
| Mytilid A                       | .. | .. | .. | + | . | . | . | . | + | + | + | + | . | . |
| Anomiacea                       | .. | .. | .. | . | + | . | . | + | + | + | + | + | + | + |
| <i>Cyprina islandica</i>        | .. | .. | .  | + | . | . | . | . | . | . | + | + | + | . |
| (? <i>Spisula subtruncata</i> ) | .. | .  | .  | + | . | . | . | . | . | . | + | ● | * | + |
| (? <i>Spisula elliptica</i> )   | .. | .  | .  | . | . | . | + | . | . | + | ● | ■ | + | + |

+ = 1-9 blocks ; \* = 10-19 blocks ; ● = 20-29 blocks ; ■ = 30 blocks or over.

The grouping employed in the table will have to be reviewed as data accumulate in later years, but larvae seem to fit more or less well into six groups. In three groups there is only one main breeding season, (a) in spring, (b) in summer, or (c) in autumn/winter. Breeding may extend over many months as in *Zirfaea crispata*, *Glycymeris glycymeris* and particularly in *Cultellus pellucidus*, but the period of the main breeding is distinct. In the three remaining groups there are two recognizable breedings ; (d) a major spring and a minor autumn, (e) a summer and autumn and (f) a minor spring and a major autumn breeding. These double breedings will be discussed later (p. 124).

Werner (1939) has collected together the earlier information on the breeding season of lamellibranchs in the North Sea, and it can be seen from his list that little information is available. Lebour (1938) lists the breeding season of many Plymouth lamellibranchs, but in several cases this is judged by the presence of ripe sperm and eggs. Thorson (1946, p. 422) comments, however, that ripe sexual products may be present for a long time (months) before being shed, and successful artificial fertilization may take place outside the actual breeding season. Jørgensen (in Thorson, 1946) gives the monthly frequency of larvae in the Sound (Øresund), but his table must be reconsidered in several cases in view of the alternative identifications in Rees (1950).

#### Notes on Species.

It does not seem necessary to describe in detail the distributions, which, it is hoped, will be sufficiently clear from the charts and from Table I. Some notes on species are given below. The following species have received no comment : *Musculus marmoratus* (Plate VI), *Cyprina islandica* (Plate VI), *Kellia suborbicularis* (Plate VI), (? *Lepton squamosum*) (Plate VI), *Mya truncata* (Plate VIII). The distributions of a few species have not been charted but have been noted in the text.

*Glycymeris glycymeris* (Plate VI).—The larvae were widespread and comparatively numerous, far more widespread than the charted distribution of the adults suggests; also they, certainly, were not all derived from the north-west, where the adult records are concentrated, since they were found as early as August in the Southern Bight. However, the adult *Glycymeris* has also been found off the east English and Belgian coasts (Haas, 1926). Ford (1923) defined *Glycymeris*



as an inhabitant of gravel deposits, and such gravel deposits cover wide areas down the east English coast, right into the Southern Bight (Borley, 1923). Since its distribution in depth ranges from 30–150 m (Haas, 1926), it would seem that there is an abundance of favourable areas for the species, at least on the western side of the North Sea. Stephen obtained 12 per m<sup>2</sup> in C18 (private communication).

(? *Limopsis*) (Plate VI).—If this should in fact prove to be the larva of *Limopsis* the relative abundance of the larva is unexpected. The Forth observations were made in September–November, the southern ones in November. Such a distribution suggests invasion from the north.

Of the two North Sea species of *Limopsis* the larva is most likely to be of *Limopsis aurita*. This has been found only north of Shetland Islands, and Schrader (1911) suggests that it is in process of dying out. If the identification of the larva is correct the species appears to be, on the contrary, still vigorous.

*Mytilus edulis* and *Modiolus modiolus* (Plate VI).—The main concentration of *Mytilus* occurred off the Danish coast, that of *Modiolus* off the Forth. Regarding both, but *Modiolus* especially, it should be noted that the Leith-Skagerrak line started some 90 miles from the Forth in August and September.

Only three localities for adult *Mytilus* are given by the four authors whose results are being plotted here, but records of *Modiolus* are much more frequent. Despite the fact that Schrader (1911) frequently collected epifaunal species, it must be considered that such species were very inadequately collected. Dense colonies of *Mytilus edulis*, of course, occur in coastal areas, and some of the larvae arising from these colonies may well be carried into offshore water.

*Adula simpsoni* (Plate VI).—No larvae were observed prior to 1949. Stephen (1927) found adults on a skull of a bottlenose whale taken 210 miles north-east of May Island, Firth of Forth, whale skulls being its normal habitat.

MYTILID A (Plate VI).—The distribution of the adult *Modiolus phaseolina* is given in the chart.

*Crenella* sp.—Only a single specimen has been found, about 30 miles off the Danish coast in May.

PECTINIDS.—*Chlamys striatus* was obtained in the tank residue<sup>1</sup> of the Leith-Skagerrak line in August.

Pectinid B was obtained 200 miles east of the Forth in December. In 1948 it was obtained in the tank residue of the Leith-Skagerrak line (October), the Hull-Copenhagen line (September) and Hull-Bremen line (October).

Pectinid D was obtained on the Hull-Copenhagen line 40 miles from the Humber in October, 140 miles away in November, and also 20 miles off the Forth in October.

Pectinid E was obtained 100 miles east of the Forth in June.

<sup>1</sup> A small proportion of the plankton caught during any tow may be washed off the silk and found in the bottom of the formalin tank of the Recorder into which the silk is wound. Although it is not possible to declare at what point in the tow this plankton was taken, it provides a source of material for qualitative analysis.

Pectinid F was obtained 80–100 miles east of the Forth and 40 miles south of the Shetlands in September.

Schrader (1911) gives the distribution of several species.

*Lima* sp. (Plate VI).—All the larvae plotted in the chart appeared to be the same species, but it is possible that there were more than one.

Anomiacea (*Monia squamula* and *Heteranomia ephippium*) (Plate VI).—The two species were not separated, but it is worth while showing the distribution of the larvae, since both the species are epifaunal. The division of larvae between epifaunal, boring and burrowing lamellibranchs is of interest and will be considered below. The south-west Dogger observations were made in November, suggesting an occurrence there due to water movements, the larvae coming from the north.

The distribution of the adults of all species combined of Anomiacea, as given by Schrader (1911), is shown.

*Myrtea spinifera* (Plate VI). The occurrence of the larvae resembles that of (? *Limopsis*), having been found on the Leith-Skagerrak line in September and October and on the Hull-Copenhagen line in November. It was suggested that the distribution of (? *Limopsis*) was due to transportation southwards from the north-west North Sea. Taking into account the distribution of adult *M. spinifera* such an explanation seems even more likely in this case. The adult was found in most of the squares in the north-west between the Shetlands and Aberdeenshire. Stephen (1933) obtained 12 per m<sup>2</sup> in C15.

*Montacuta* (*Montacuta bidentata* and *Mysella substriata*) (Plate VI).—In the charts labelled “*Montacuta*” both these species are included. (Throughout the text “*Montacuta*” refers to both species combined.) The overall plot for 1948 is given to show that higher numbers were obtained in this year than in 1949. The distribution of adults of both species is shown in the 1948 chart. Schrader (1911) gives a chart showing his records for each species separately. Davis (1925) obtained 2 per m<sup>2</sup> of *Montacuta bidentata* in J10.

*Montacuta ferruginosa* (Plate VII).—This larva was more frequent in 1949 than in 1948. Davis obtained about 2 per m<sup>2</sup> in J7.

*Cardium* sp. (Plate VII).—In the chart for *Cardium* A the distribution of adult *C. ovale* is given, for *Cardium* B the adult *C. minimum*, and for *Cardium* D the adult *C. echinatum*. It is to be understood that there are no other reasons for linking the larvae and adults than are given in Rees (1950).

Two records of adult *C. ovale* near Fair Isle and another north of Flamborough Head are not shown in the diagram.

VENERIDS A and B (Plate VII).—The larvae of Venerid A have been linked, rightly or wrongly, with the adult *Venus ovata*, and Venerid B with the adult *V. striatula* as in Rees (1950). The consideration of the distribution suggests, in fact, that the linkages should be reversed, but the evidence is still insufficient.

The larvae of Venerid A occurred earlier than Venerid B, in September and October, with October being the peak month; Venerid B occurred in October and November with the latter as peak. Davis (1925) obtained 2 per m<sup>2</sup> of *V.*



*striatula* in K12. The density of *V. ovata* was very low. Stephen (1933) obtained 5 per m<sup>2</sup> of *V. striatula* in H15 and K12 and 5 *V. ovata* in L12.

VENERIDS C-F (Plate VII).—The larvae of each kind occurred very infrequently and are combined in one chart.

(? *Paphia*) (Plate VII).—No species of *Paphia* is listed by the authors in dealing with the distribution of adults.

(? *Mactra corallina*) (Plate VII).—The highest densities of adults were found by Davis (1925) to be in the south-west part of the Dogger. High densities were very localized. The overall density in F7 was 251 per m<sup>2</sup>.

(? *Spisula solida*) (Plate VII).—The spatial distribution of the larvae was very similar to that of (? *Tellina crassa*). They were obtained in May and April and again in September. In 1948 they were found from September to November in the same region.

As regards the adult we cannot include the findings of Schrader (1911), since he lumped *S. elliptica* and *S. solida* together. Stephen (1933) gives a chart of the adult distribution. This chart includes Petersen's (1914) records of *S. solida* off the Danish coast. It would be fair to neglect these records, since Petersen, too, lumped *elliptica* and *solida*. Davis (1925) found nearly 2 per m<sup>2</sup> of *S. solida* in G3.

(? *Spisula subtruncata*) (Plate VII).—In view of the extremely high densities of adult *S. subtruncata* found by Davis (1925) it is surprising that the larvae should have been found in comparatively small numbers only. This was also true in 1948. The persistence of a larval population, though low in density, over the Great Fisher Bank, compared with the distribution of adults, is of interest in view of Marshall's (1948) suggestion that the Fisher Bank population in 1938–39 may have been due to translation of more southerly species northwards. Davis (1923) gives great detail on patches of the species. The overall density in G9 was 424 per m<sup>2</sup>.

(? *Spisula elliptica*) (Plate VII).—This larva was easily the most common of all, reaching concentrations many times denser than any other species. Its great density would lead one to expect it to be *S. subtruncata*. It is not so identified because, however uncertain it may be that Kändler's (1926) and Jørgensen's (in Thorson, 1946) species agree with the larva named here as (? *S. subtruncata*), there can be no doubt that their larva is not this one. The square end of (? *S. elliptica*) is quite distinctive and unmistakable as emphasised by Rees (1950).

Concentrations of 1949 may be compared with those of 1948. The population off the Skaw was well developed in 1948, somewhat better developed than in 1949 and with August the peak month, two months earlier than in 1949. The north-east Dogger concentration of October, 1949, was very great, larvae of (? *Spisula elliptica*) being present to the extent of more than 5000 per 10-mile block. The 1948 Great Fisher Bank concentration was small.

The distribution of adults is repeated from Stephen's (1933) chart with the slight modification of taking Petersen's "*Spisula solida*" to be *S. elliptica* since he did not separate the two. Schrader (1911), also, did not distinguish *S. elliptica*. The number found by Davis (1925) was very low, much less than 1 per m<sup>2</sup>. Stephen



(1933), on the other hand, found high numbers off the Danish coast. He has kindly provided further details beyond those published. These include densities of *S. elliptica* of 35 per m<sup>2</sup> in L13, 15 in N13 and 10 in O14.

MACTRID E (Plate VII).—The larva was recorded off the Skaw in November. All the other records were obtained in April and May (when the Leith-Skagerrak line was not sampled).

In view of the suggestion in Rees (1950) that this may be the larva of *Spisula truncata* the two records of the adult *S. truncata* (Schrader, 1911) are given, but it must be recognized that only Schrader, of the four authors with whose distributions we are concerned, separated *truncata* from other forms of *Spisula*.

(? *Lutraria lutraria*) (Plate VII).—It is by no means certain that only one species has been included in this group. Since records are so few any errors that may have arisen are not important.

Only Davis (1925) found the adult, at a density of 1 per m<sup>2</sup> in G7.

*Tellina fabula* (Plate VII).—The larva occurred infrequently. Specimens were obtained in the tank residue of the Leith-Skagerrak line in July. It was noted twice on the silk in 1948, midway along the Hull-Copenhagen line in August and again in September. Davis (1925) obtained over 3 per m<sup>2</sup> in G6 and G7.

(? *Tellina pygmaea*).—The larva was only twice noted on the silk, once off the Skaw in July, 1948, and again in June, 1949. Larvae were also obtained in the tank residue of the Hull-Copenhagen line in November.

(? *Tellina crassa*) (Plate VII).—The larvae were found only in the southern North Sea, in the same region as (? *Spisula solida*), and all in September. They were present in relatively high numbers over a short period. A high proportion of the specimens were very large, the dissoconch having begun to form.

There are only two records of adults, one by Davis (1925) in the north-west corner of the Dogger Bank, and one by Schrader (1911) 20 miles south of the Shetlands.

*Abra prismatica* (Plate VIII).—This species was more abundant in 1949 than in 1948. Davis (1925) obtained 2.5 per m<sup>2</sup> in J9 and Stephen (1933) 8 per m<sup>2</sup> in G15 and H12.

*Abra nitida* (Plate VIII).—Davis (1925) obtained slightly less than 1 per m<sup>2</sup> in C9.

*Abra alba*.—The larva was not found in 1949, but was obtained on the eastern ends of the two Hull-Bremen lines taken in October, 1948. It was also obtained in the tank residue of the Hull-Rotterdam line in October, 1947.

Stephen (1933) charts the distribution of the adult. Schrader (1911) provides no additional records. Taking regard of the distribution of the adults and the coverage of the Recorder lines it is not surprising that so few larvae have been obtained.

(? *Donax vittatus*) (Plate VII).—All three observations of this larva on silk were made on September records. The tank residue of the July Leith-Skagerrak record had a good number of specimens, a fact that may have resulted from the

Recorder being shot well inside the Forth on this occasion, although none were found on the silk pertaining to this part. Davis (1925) obtained 6 per m<sup>2</sup> in H4.

*Ensis ensis* (Plate VIII).—Larvae were occasionally found in the tank residue of the Aberdeen-Lerwick line. Davis (1925) obtained 1.7 per m<sup>2</sup> in M9, but considered that the species was inadequately collected. Petersen (1914) obtained 8 per m<sup>2</sup> in M12.

*Ensis siliqua* (Plate VIII).—This was of occasional and scattered occurrence appearing at the same season as *E. ensis*. Records of adults show that this species was rare in comparison with *E. ensis*.

*Cultellus pellucidus* (Plate VIII).—The larva was found in every month, but, up to August, it was mainly confined to the east central North Sea, off the Danish coast. Its distribution spread considerably in September, to reach its peak in October. It is of interest how, in the direction Hull to the Skagerrak, the observations in November and December form five distinct pairs. Davis (1925) obtained over 14 per m<sup>2</sup> in L10.

*Hiatella arctica* (Plate VIII).—Only Schrader (1911) gives information on the distribution of the adults.

In 1948 the highest numbers also occurred off the Forth, but in this year in August–September rather than in September–October as in 1949.

*Hiatella gallicana* (Plate VIII).—Records of the adult are comparatively rare. This may be partly due to the fact that it bores into soft rock and is therefore inadequately sampled. However, the larvae do give the same sort of picture, and it is quite clear that the larvae of *H. arctica* are much more common than those of *H. gallicana*.

MYACEAN B (Plate VIII).—This larva was found more abundantly than either *H. gallicana* or *H. arctica* off the Aberdeenshire coast. The only other record was about 120 miles off the Forth, a record that may well have resulted from transportation of the larvae from the coastal area.

*Aloidis gibba*.—Larvae were obtained in April only, midway between the north-east Dogger and the Danish coast, on the Hull-Copenhagen line.

From the results of Davis (1925) and Schrader (1911) the *Aloidis* area of the North Sea may be roughly defined as the eastern half of the North Sea south of the Hull-Copenhagen line and north of the Hull-Bremen line. Davis obtained 2.5 per m<sup>2</sup> in J7.

*Zirfaea crispata* (Plate VIII).—Larvae were absent only in the months July to September. The main Dogger Bank concentration occurred in April and May.

(? *Pholas dactylus*) (Plate VIII).—October was the peak month in 1948, a patch occurring along the southern edge of the Dogger almost identical in extent with that of November, 1949.

(? *Barnea candida*) (Plate VIII).—The larval distribution is similar to that of (? *Tellina crassa*) and (? *Spisula solida*).

*Teredo* sp.—The *Teredo* larva described in Rees (1950) was obtained 80 miles off the Forth in October.



(? *Thracia*).—Larvae have been seen only in tank residues, in those of the Hull-Bremen line in October and November, 1948, and the London-Copenhagen line in November, 1948. It was not observed in 1949.

(? *Lyonsia*) (Plate VIII).—April was distinctly the peak month.

## DISCUSSION.

### General.

Such a survey as this, involving the pelagic larvae of bottom-living adults, raises the major question of the association between the distributions of the larvae and the parent adults. Another important question, the answer to which is the main purpose of this work, is the possibility of forecasting the distribution of the future adult population. For this first report the available information is clearly inadequate to deal with these questions. The distribution of the larvae has been thoroughly traced for one year only, and this year may well have been unusual. The insufficiency in information, however, is not confined solely to the larvae. There is a complete lack of information about the contemporary bottom fauna over the general North Sea, and widespread surveys have not been undertaken since the early 1920s. Considerable changes in the bottom fauna may have occurred since then.

Nevertheless, this is the first time that a survey of lamellibranch larvae of this nature has been attempted, and it is believed to be worth while to issue the results of this first year rather than wait for several years in the hope that these questions may be considered more adequately.

It would enlarge our understanding of the distributions if the factors determining the onset of breeding, presumably the critical spawning temperatures (Orton, 1920), and the apparent double breeding periods each year of a few species, were known for each species. Though this information is required to explain the distributions shown by the Recorder, the Recorder technique is not suitable to derive it. Such questions are best answered by direct observations of the adults.

However, one encouraging feature has been brought to light—the consistency in distribution. Attention has been directed to this in the distribution of the high densities of larvae (p. 107). Such a consistency is very clearly marked, too, both in the distribution of single species and the distributions of groups of species. This is a feature of such considerable importance that it is worth while giving several examples: (a) *Glycymeris glycymeris* (Plate VI) off the Aberdeenshire coast in June–November and off the Humber in January and September–December, (b) (? *Limopsis*), *Adula simpsoni* and *Lima* (all in Plate VI) off the Forth in September–November, (c) Anomiacea (Plate VI) off the Aberdeenshire coast in June–November, (d) *Monacuta ferruginosa* (Plate VII) over the Great Fisher Bank in July–October, (e) *Cardium* D (Plate VII) near the Great Fisher Bank in September–November, (f) (? *Spisula subtruncata*) (Plate VII) in the south-west Dogger in October–December, (g) (? *Tellina crassa*), (? *Spisula solida*) (both in Plate VII) and (? *Barnea candida*)



(Plate VIII) in the Southern Bight, (h) *Zirfaea crispata* (Plate VIII) along the southern edge of the Dogger Bank in April, May, October and December.

These examples form only a short selection.

Thus a definite pattern emerges, raising the hope that the distribution may be explained in terms of permanent or semi-permanent factors. The 1948 results are so well in keeping with those of 1949 (except that the numbers of individual species were higher in one year than the other) that we may justifiably speak of the characteristic larval communities of the various localities.

#### *Distribution of Total Lamellibranch Larvae.*

In the chart of larval distribution (Text-fig. 2) the density of adults is indicated by means of dots, one dot representing 5 adults per m<sup>2</sup> per international square. The adult densities are repeated from Marshall (1948) with the addition of Petersen's results (p. 111), and it should be noted that these adult densities were determined prior to 1925. The correlation between high adult and larval densities is poor. It is even less satisfactory when it is realized that the high density adult area south-east of the Shetlands is of no relevance, since it was mostly made up of *Thyasira flexuosa* (Stephen, 1933), which has no pelagic larvae. That patch would, in fact, disappear if only adults with pelagic larvae were considered.

Orton (1937) thought that *Cardium edule* and other organisms become concentrated in the plankton in localities where slack and eddy waters occur, and settle in vast numbers in such localities. He predicted that a rich planktonic area would be found over the north-east region of the Dogger, in the north-east Dogger Swirl. This prediction has proved correct for lamellibranch larvae, concentrations having been obtained near there in several years and, in fact, one of the highest densities ever obtained during the Recorder survey occurred there in 1949.

The existence of swirls will go a long way towards explaining the distribution of larval patches shown in Text-fig. 2. A comparison of this figure with the generalized water circulation given by Böhnecke (1922) and Tait (1937) shows, in particular, that major patches fit in with the south-west and north-east Dogger Swirls and with the Great Fisher Bank (Lindesnaes) Swirl. These swirls vary substantially in position, but are in part dependent on geographical features, the elevation of the Dogger Bank and narrow opening of the Skagerrak (Böhnecke, 1922), and we may regard these geographical features as being indirectly the permanent features determining the consistency in distribution of total lamellibranch larvae referred to above (p. 107). It can be supposed that the region from the south-east Dogger to the Great Fisher Bank may be covered by a swirl system at some time throughout the year, since in summer the north-east Dogger Swirl and Lindesnaes Swirls merge and another swirl develops south-east of the Dogger (Böhnecke, 1922). Tait (1937) says that in 1912 the north-east Dogger Swirl almost certainly travelled northwards in May-July to coalesce with the Lindesnaes eddy. It is clearly not to be expected that year after year a particular area will be marked out as a swirl by a concentration of larvae. Perhaps larvae may not be present to congregate,

or perhaps the swirl may have moved away from the sampled area or even have disappeared.

It is doubtful if all the patches in Text-fig. 2 can be explained by swirls. There is a likelihood that the limited patches west of the Great Fisher Bank are some-

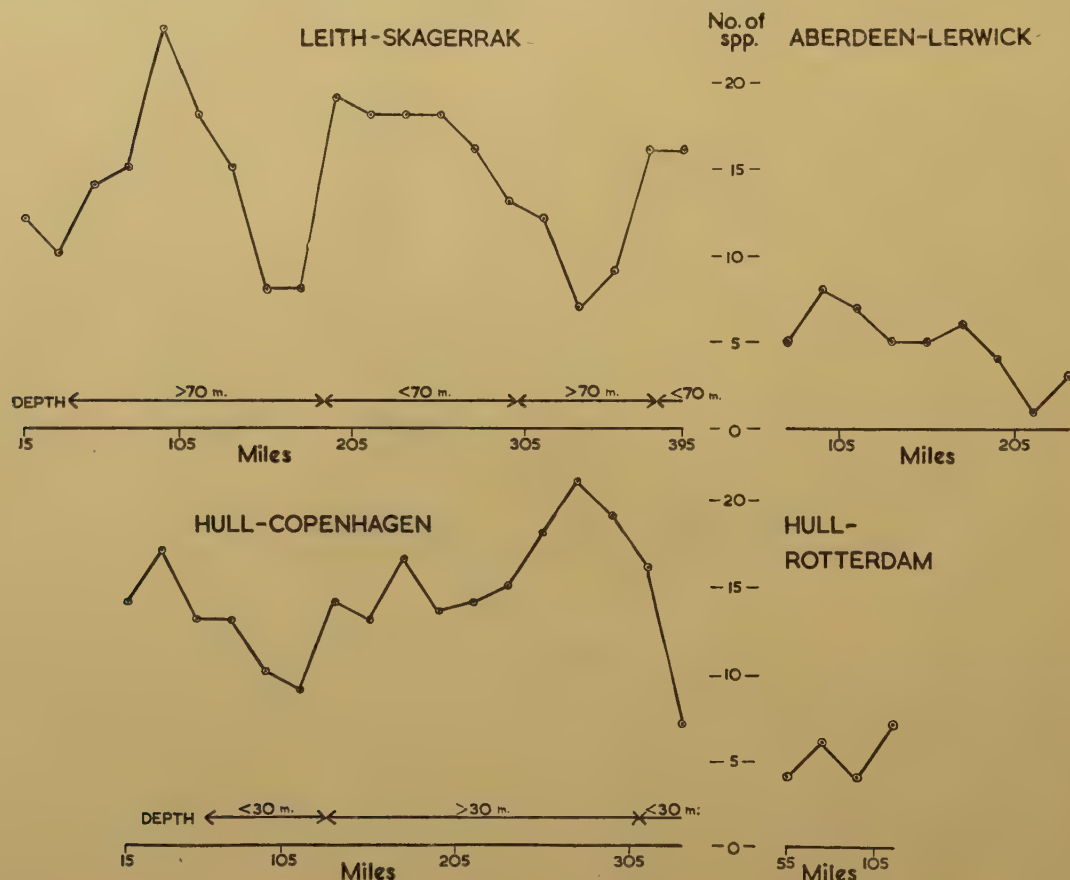


TEXT-FIG. 4.—Chart showing distribution of 10-mile blocks with over 1000 lamellibranch larvae, repeated from Text-fig. 2, superimposed on a sketch map of deposits containing mud (dotted areas), derived from Close's Fishermen's Chart. The boundary of a silt area, derived from Borley (1923), is shown as a hatched line. Gaps in the boundary lines result from insufficient information.

how related to stream currents (cf. Tait, 1937, p. 54). However, this must remain a problem involving the whole plankton complex, and it is hoped to study this aspect in a later 'Bulletin.'

A line of approach to this question of larval distribution can be made through the bottom deposits. Borley (1923) mapped in great detail the deposits of the

southern North Sea. Equally suitable data north of lat.  $56^{\circ}$  are not available and, instead, a sketch map, derived from Close's Fisherman's Chart, is given in Text-fig. 4, of the areas of deposits containing mud, whether listed as "sand and mud," or "mud" or "ooze." Superimposed on that derived from the Fisherman's Chart is the boundary of the large area of silt south of the Dogger as derived from Borley (1923).



TEXT-FIG. 5.—Graphs showing the number of species obtained on each analysed 10-mile block on four Recorder routes in 1949. The position of the 10-mile blocks can be seen by comparing the horizontal scale of miles with the chart in Text-fig. 1 of 'Hull Bulletin' 7.

There seems to be a correlation between high larval densities and the presence of muddy deposits (cf. Text-fig. 1 with the silt area in Text-fig. 4). It is not suggested that the correlation is necessarily direct, through an accumulation of adults in muddy deposits. Mud is deposited where the bottom currents are weakest and one can return to Orton's view that larvae congregate in slack water or, to meet some cases, it may be better to express it negatively—larvae are not dispersed so much in slack water.



*Distribution of Species of Larvae in 1949.*

*Qualitative.*—The number of species found on each analysed block throughout the year on four Recorder lines is shown in Text-fig. 5. The depth profiles for these lines are given in 'Hull Bulletins' 1 and 7, and some of the depths are broadly indicated in Text-fig. 5. The lack of variety of species on the Aberdeen-Lerwick and Hull-Rotterdam lines is clearly brought out. The greatest variety occurred 100 miles off the Forth, on the Leith-Skagerrak line.

Though the values for the western end of the Leith-Skagerrak line are not reliable, being on the low side since the region off the Forth was not sampled in August and September, the line may be said to have three peaks and two troughs. The central peak occurred over the Great Fisher Bank, with depths less than 70 m,



TEXT-FIG. 6.—Histograms showing the number of species obtained in each month, taking in all samples from the North Sea in 1949.

and the eastern one in the Skagerrak, also over a depth less than 70 m. The two troughs occurred over depths exceeding 70 m. The western peak occurred over deep water, but this peak corresponded to the high numbers of larvae obtained, a feature which was unusual, since the high density occurred effectively only in one year (Text-fig. 1; see also total numbers for 1938 and 1949 in Text-fig. 3), and it will be maintained below that it was due to a great influx of larvae from the north. The Hull-Copenhagen line may be said to have two troughs, both over depths less than 30 m. Between the two shallow sections the depths varied down to 45 m.

Accepting, then, the unusual character of the off-Forth peak, there appears to be a rough correspondence between variety of species and depth, depths over 70 m and less than 30 m having a poorer variety.

The number of species of larvae obtained in each month over the whole North Sea is shown in Text-fig. 6. A major peak occurred in October and a minor one in June; the minimum occurred in January. Thorson (1946, fig. 196) gives a similar diagram for larvae in the Sound, the trend of which is quite similar to that for the North Sea.

The most important generalization regarding spawning is that of Orton (1920), who maintained that sea temperature must be the factor of paramount importance controlling breeding in marine animals under normal biological conditions, and that breeding is dependent on the attainment of a critical temperature which is a physiological constant for the species. It would seem that some refinement of Orton's original hypothesis is required to meet some of Thorson's (1946, p. 422) objections, but, doubtless, the main features of the hypothesis will remain.

Little is known about critical spawning temperatures in lamellibranchs, apart from the various species of oyster. Nelson (1928a) gives  $10^{\circ}$ – $12^{\circ}$  as the critical temperature in *Mytilus edulis* and *Mya arenaria*. However, the higher the temperature the greater must be the number of species of lamellibranchs whose minimum critical temperature for spawning is exceeded. This would seem to account satisfactorily for the main peak in the number of species in October, a short time after the attainment of the highest temperature of the year in the North Sea.

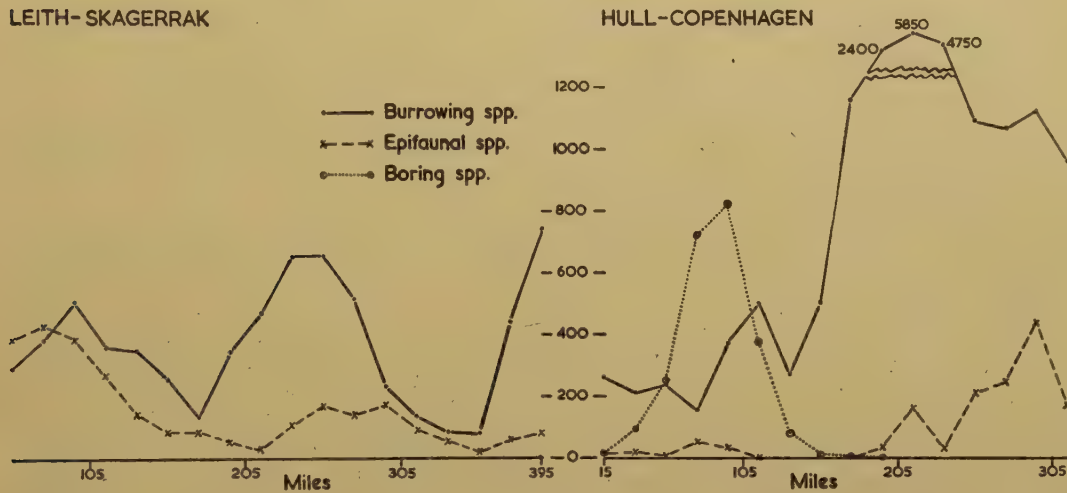
Relevant to the question of temperature and spawning is that of the spring and autumn breedings in a few species. Orton (1920, p. 345) states that many animals continue to breed so long as the temperature remains above a certain value. It would appear that the species with a double generation are not amongst these, since the temperature continued to rise after the spring spawning, during the period when no larvae were found. If temperature is the trigger to spawning in these species in spring, is it the trigger to spawning in autumn? According to Orton (1920) *Patella vulgata* breeds at about the maximum temperature and again at the minimum. Thorson (1946, p. 422) accepts this system for *Polydora ciliata*. On the face of it, however, this seems to be a peculiar phenomenon, and one may feel hesitant in advancing such an explanation of the case of the species we are dealing with. It is possible that the spring spat grows to maturity rapidly and spawns again within a few months. A rapid attainment of maturity is known in some species. Thus *Heteranomia squamula* (= *Anomia aculeata*) gives larvae on being fertilized at an age of less than four months (Orton, 1914), and it is probable that both *Abra alba* and *Cardium ovale* mature in summer in about three to four months (Orton, 1924). This, however, may not be a satisfactory explanation in those species with a minor spring and a major autumn breedings, e.g. (? *Spisula subtruncata*) and (? *S. elliptica*) (Table I). In these cases the main adult population possibly spawns twice, a quiescent period intervening whilst the sexual products mature.

In the case of *Mytilus edulis*, which had a peak of frequency in June–July and again in November, it is known that maturity is reached after one year (Field, 1923). However, Jensen and Spärck (1934, quoted by Thorson, 1946, p. 426) found that the older specimens breed in spring whilst the younger ones spawn later in the year.

*Quantitative.*—It should be noted that the relative numbers of the larvae of the various species do not give a true picture of the relative numbers of the corresponding species of adults in the North Sea, since some important species have

non-pelagic larvae or larvae which are pelagic for a very short time only. Also, even in the case of species having pelagic larvae there is a difference in fecundity in the different species and a difference in time during which the larvae are pelagic. Of the species with no pelagic larvae which appear to be frequent in the North Sea, the species of the Nuculacea, *Modiolaria nigra*, *Astarte sulcata* and, above all, *Thyasira flexuosa*, may be mentioned.

Accepting, then, the fact that the relative numbers of larvae are not equivalent to the relative numbers of adults, a list is given of the ten most common larvae found. The number in brackets following the specific name refers to the number of hundreds of larvae estimated as collected by the Recorder in 1949. In order of frequency the list is: (? *Spisula elliptica*) (140), *Cultellus pellucidus* (26), *Zirfaea*



TEXT-FIG. 7.—Graphs showing the yearly number of larvae of epifaunal, burrowing and boring species obtained on each analysed 10-mile block of the Leith-Skagerrak and Hull-Copenhagen lines. The position of the 10-mile blocks can be seen by comparing the horizontal scale of miles with the chart in Text-fig. 1 of 'Hull Bulletin' 7.

*crispata* (23), *Abra prismatica* (21), *Glycymeris glycymeris* (20), *Ensis ensis* (20), *Mytilus edulis* (18), *Montacuta ferruginosa* (17), *Modiolus modiolus* (13), *Hiatella arctica* (11).

The very great dominance of (? *Spisula elliptica*) in 1949 was probably an unusual feature; in 1948 the comparable value was probably under 40. It may be mentioned, in addition, that the 1949 value for (? *Spisula subtruncata*) was 9.

Of these ten species, three are epifaunal (*Mytilus*, *Modiolus* and *Hiatella*) and one a borer (*Zirfaea*). To follow up this point, all the larvae obtained in two lines throughout the year have been separated into the three ecological groups, the burrowing, the boring and the epifaunal species. Text-fig. 7 shows the total number of larvae of each group on each analysed block of two lines.



On the Leith-Skagerrak line only the larvae of burrowing and epifaunal species realized appreciable numbers. It will be seen that the off-Forth peak (cf. Text-fig. 3) was made up of approximately equal numbers of both groups. Over the Great Fisher Bank the burrowing species easily predominated in 1949, but in years with a pronounced concentration of larvae over the Bank epifaunal species probably form a very substantial part of the total population. Epifaunal species formed a very minor part of the Skagerrak patch (4, Text-fig. 1). On the Hull-Copenhagen line the larvae of boring species, *Zirfaea* and *Pholas*, predominated over the shallow water of the south-west Dogger. Epifaunal species were almost absent over the Dogger, but increased in numbers towards the Danish coast. The epifaunal species, however, remained very low in comparison with the larvae of burrowing species along the eastern half of the line.

*The influence of water movements.*—In approaching the question of the influence of water movements on the distribution of larvae it is necessary to consider, first of all, the duration of pelagic life. The distances that larvae may be transported are determined by this factor and on the velocity of the water. Since no estimates of duration can be made from the foregoing results we are dependent on judging from the previous literature on the subject.

The most general statement that has been made is that from Jørgensen's calculations, which seem to show an average pelagic life of 3–4 weeks in summer-spawning species and four to six weeks in winter-spawning species of lamellibranchs (Thorson, 1946, p. 455).

Some estimates of durations under natural conditions may be given: *Mytilus edulis* four weeks and *Mya arenaria* two weeks in the Isefjord, temperature not known (Thorson, 1946, p. 453); *Mytilus edulis* and *Mya arenaria*, presumably under normal conditions and at a temperature below 20° C., three weeks (Nelson, 1928b); *Cumingia tellinoides* three weeks at 20°–21° C. (Grave, 1927). Larvae of shipworms last at least a month, perhaps more (Sigerfoos, 1908). *Teredo navalis* takes five weeks between spawning and settling at Woods Hole (Grave, 1928). The total larval life of *Ostrea lurida* is at least forty days at 17°–18° C. (Hopkins, 1937).

Much information is available about larval development in oysters. The literature has been reviewed by Korrinda (1941), and is of interest in showing the general slowing down of development with decrease in temperature. As examples we may take firstly *Ostrea virginica*, which is non-incubatory—thirteen days at 23°–25° C., fifteen days at 21°–22° C. and seventeen days at 20° C. As a second example we can take *Ostrea edulis*. The larval life of this is divided into an incubatory phase lasting about ten days (more or less) and a pelagic phase. The pelagic phase at 22°–23° C. was six days, at 21° C. seven days, at 19° C. twelve days, at 16° C. fourteen days (Korrinda, 1941, p. 134), *i.e.*, the pelagic life was doubled with a temperature change from 23° C. to 19° C.

All the examples are at relatively high temperatures, and it is generally agreed that the lower the temperature the greater the duration of the pelagic life. Most

of the larvae dealt with in this report grow under much lower temperatures, at least during part of their breeding period. It is impossible to give precise values, since the whole range from surface to bottom is involved at any one time. However, the difference from the above results may be appreciated when it is realized that larvae develop during March, April and May at temperatures of 5°–10° C.

In the absence of more useful information it seems reasonable to expect a pelagic life of 6 weeks or so for larvae settling at 350–400 $\mu$ . Indication of the surface drift velocities of the northern and middle North Sea may be obtained from Tait (1937, figs. 45–47). For purposes of illustration it is fair to work on an average drift velocity of 8 miles a day (the top velocity is over 12½ miles per day). At this rate a larva spawned off Aberdeen could reach the Humber in about 25 days and if spawned just south of the Shetlands in about 43 days. It is clear, therefore, that larvae may be transported considerable distances in the North Sea, even allowing for marked variations in duration and velocity.

The distributions of several organisms, as shown by the Plankton Recorder, have been explained by a progressive translation from the north-west towards the southern North Sea (Rae and Rees, 1947; Marshall, 1948), the explanation being based on the current system described by Böhnecke (1922) and Tait (1937). These "north-west indicator" species follow approximately the same pattern. In August they are concentrated in the north-west and, subsequently, appear off the Forth in September–October and off the Humber in November–December. Allowing for the fact that larvae spawned in the path of a prevailing drift are too small to be identifiable during the first part of their journey, the larvae of (? *Limopsis*) and *Myrtea spinifera* appear to conform to this pattern of distribution. Though a composite group, the Anomiacea also conform. It will be suggested below that the larvae of *Modiolus modiolus* and *Musculus marmoratus* off the Humber in October were also translated from the north. The alternative explanation that there was a succession in time of spawning is hardly likely in these cases. If the initial stimulus to spawning is the attainment of a certain critical temperature (Orton, 1920), then, at this time of year, the succession in breeding should have been from south to north, whereas the succession in distribution was from north to south.

Instead of dealing with individual species we can consider the composition of patches shown in Text-fig. 1, with particular attention to the influence of water movements on them. This may be done, at present, only briefly and tentatively, but it is hoped to continue this work for some years and initial consideration of the data will serve as a useful background. The distributions will become very much clearer when knowledge of the contemporary bottom fauna, now being investigated at other laboratories, becomes available.

*Patch 1* (Text-fig. 1).—This patch occurred very distinctly in 1938 and 1939, and only in 1947 in post-war years. In all these years it occurred in July, and there is little doubt that the population was mainly of epifaunal origin, chiefly



*Mytilus edulis*, but also *Modiolus modiolus*, *Hiatella arctica* and Anomiacea. It might well have been a swirl concentration (cf. Tait, 1937).

*Patch 2.*—This patch, occurring effectively only in 1949, was unusual. As far as the results go October was the important month, but it should be noted that the August and September lines did not start until some 80 miles from the Forth and the results are thus incomplete.

On the same record that had the main concentration of larvae the number of *Metridia lucens* was unusually high, much higher than obtained at any time in 1938 or 1946–48. The peak number occurred, too, earlier than in these years. Similarly, the peak number of *Candacia armata* in 1949 was much greater than in these previous years. The absence of collections near the Forth in August and September restricts the amount of guidance to be derived from these two useful north-west indicator species but the higher numbers of the two species appear to be associated with the Forth lamellibranch larval concentration. Dr. Tait has kindly informed me that he found that the southward movement of oceanic (or Atlantic) water into the North Sea reached its greatest intensity and penetration in August, in 1949. That this should occur in August is unusual, the maximum intensity of the autumn usually occurring later in the year. It appears, therefore, that the influx was earlier than usual, and occurred at a time when larvae, particularly of the epifaunal species *Modiolus modiolus* and *Hiatella arctica*, were still abundant. The early October community off the Forth consisted of 55% of epifaunal species and over 30% of *Glycymeris glycymeris*, whose adults were found in abundance in the north-west (Stephen, 1933). It can hardly be doubted that had the Forth end been sampled in September the early effect of invasion would have been shown, as may be seen from the distribution of *Adula simpsoni* and *Lima* (Plate VI). Several specimens of *Adula simpsoni* were found in the tank residue of the Leith-Skagerrak line in the autumn of 1949; it is significant that none were found in the tank residue in 1946–48 (since the silk collections were not analysed in these years, this is the only comparable information). The same southerly movement of water probably accounted for the October records of *Modiolus modiolus* and *Musculus marmoratus* off the Humber (Plate VI); it was noted during analysis that these specimens of *M. marmoratus* were unusually large.

Had the influx been delayed by, say, a month, the seasonal decrease in number of larvae would have removed the possibility of a Forth concentration appearing.

*Patch 3.*—The Great Fisher Bank concentration was poorly developed in 1949 in comparison with 1938, 1939 and 1948. The average number of larvae over the Bank in 1939 and 1949 (Text-fig. 3) was not greatly different in the two years, but when individual records are considered there was a pronounced difference between them. The June and July records of 1938, the June record of 1939 (Marshall, 1948) and the July record of 1948 had high numbers, records in other months being low. In 1949 no high density was recorded, but there was a persistent moderate density from July to October, the highest number being about one-tenth of those obtained in the peak concentration of earlier years.



It is unfortunate that no major concentration was obtained in 1949 since the data for 1948 are far from complete. It appears that the high density in early July of 1948 was due in large part to a high number of larvae of epifaunal species, chiefly *Modiolus*. Whilst preparing this paper the results for the earlier part of 1950 have become available and these have shown a very good development of the Fisher Bank population. In mid-May *Mytilus edulis* larvae were easily predominant, comprising over 70% of the population ; by the end of May *Mytilus edulis* had dropped to 35% and larvae of *Ensis* rose to over 40%. By June 10th the population had changed considerably, and Venerid D was the most common larva with *Abra prismatica* second. There were no less than 16 species in the well-marked Bank concentration of June 10th, 1950. No Bank concentration was shown on the record taken on July 8th.

There is, of course, nothing unexpected in this change of composition of the population with time. Such a change occurs through the normal seasonal succession of species and does not, in itself, imply a change in locality of origin of the population.

Marshall (1948) suggested that the Great Fisher Bank concentrations might be due to adult populations of the north-east half of the Dogger Bank, and that, in this case, a fair proportion of larvae of *Spisula* would be expected. As far as the main concentration is concerned this suggestion is not borne out. The Bank concentration has occurred within the May-July period, when *Spisula* larvae are low in number, and it is known that some of the main concentrations have been due to epifaunal species. Larvae of (? *Spisula subtruncata*) and of (? *Spisula elliptica*) have occurred over the Bank (Plate VII) even as early as June (1950), but never to an important extent. It is quite possible that these few larvae may have been brought from the south-west, but it is to be noted that (? *Spisula subtruncata*) larvae have also been found 100 miles from the Forth ; a southern origin of these is most unlikely. There is, probably, a local population of *Spisula elliptica* in the Fisher Bank.

There seems to be an association between *Clione* and high larval densities over the Fisher Bank, though the appearance there is not exactly coincident in time. Thus *Clione* was found over the Bank in July, 1938 (when larvae were abundant), and in August, 1939. Also, in 1948 *Clione* was found over the Bank on July 30th, on the record following the high larval density. Marshall (1948) considered that a northern origin for Bank *Clione* is more probable than origin from the Skagerrak. Yet a Skagerrak origin is quite possible. Graham (1934) visualized the possibility that the swirl over the Great Fisher Bank could act as an agent for transporting cod fry from Norwegian coastal waters into the North Sea proper. The only suggestion that can be made at present is that the direction of origin of the larval community was the same as that of *Clione*, allowance being made for larvae arising from the local adult population ; it is still a matter of opinion that this was from the north.

*Patch 4.*—This was only slightly developed in 1949, in October, with (? *Spisula*

*elliptica*) predominant and Venus A next in numbers. Non-burrowing species amounted to about 18%. The major development of this patch occurred in June–August, 1948. Over this period “*Montacuta*” was the most numerous larva, but was exceeded in numbers slightly by (? *Spisula elliptica*) in August. Epifaunal species were present to about 40% of the population in July, falling to a very small percentage in August. The concentration may have developed at the junction of the easterly current along the Danish coast and the westerly current along the Norwegian coast. It may well be related to the high adult concentration near the adjacent coast (Text-fig. 2).

*Patch 5.*—Though this developed twice in 1949, in May–June and again in October, this is not an important patch, since previously it was obtained only in 1948, in October, and even in 1949 the density was barely above the limit chosen to define patches. Its composition leads one to believe that it was a development largely from the local bottom population.

*Patch 6.*—As mentioned above, Orton (1937) predicted larval concentrations in this area. According to Böhnecke (1922) the Dogger Bank forms the southern boundary of the north-east Dogger Swirl and, this being so, the standard Hull-Copenhagen time runs rather south of the Swirl. This larval patch may, consequently, be more truly related to the south-east Dogger Swirl, which develops on the coalescence of the north-east Dogger and Lindesnaes Swirls (Böhnecke, 1922).

Over 2000 larvae per m<sup>2</sup> were found in the centre of the patch in October, 1949, and this estimate may have been on the low side. Of this very high number (? *Spisula elliptica*) accounted for about 95%.

*Patch 7.*—Though this patch was made up mostly of *Zirfaea crispata* in 1949, there is reason to believe that larvae of *Ensis* may form a considerable part of the population in spring and early summer patches near this region in other years.

*Patch 8.*—According to Böhnecke (1922) the south-west Dogger Swirl is bounded to the north by the Dogger Bank, so it is likely that the standard Hull-Copenhagen recorder lines run to the north of the Swirl. However, the larval patch found in 1947 occurred about 15 miles north of the standard Hull-Copenhagen Recorder route. This patch was made up predominantly of (? *Macra stultorum*), together with some “*Montacuta*” and *Ensis*.

*Patch 9.*—This was obtained quite infrequently and never in really high density. In 1947 it was made up chiefly of (? *Spisula subtruncata*), together with (? *Spisula solida*) and (? *Tellina crassa*). One interesting feature of this area is the relatively great importance of species preferring coarser grades of bottom. Thus *Tellina crassa* and *Glycymeris* are given in Ford's Class B (Ford, 1923), and probably *Spisula solida* is to be considered in the same group (cf. Ford, 1925).

#### SUMMARY.

1. The distributions of high densities of larvae from year to year, and of the species of larvae from month to month, were often repeated, in such a manner as to suggest a definite pattern of distribution.



2. Many of the major patches can be related to the existence of swirls. The concentrations of larvae seem to be correlated with silty or muddy deposits, and poorly correlated with the distribution of adults as shown in previous work. Larvae were uncommon over the main part of the Dogger Bank.

3. The maximum number of species occurred in October, with a secondary maximum in June. There was a poor variety of species in the north-west North Sea and the Southern Bight. In the central North Sea there appeared to be a correspondence between number of species and depth, depths over 70 m and less than 30 m having a poorer variety.

4. Most of the species encountered had only one *main* breeding period during the year, but a few species had two distinct breeding periods.

5. Whilst, generally, larvae of burrowing species predominated, in certain parts larvae of epifaunal and boring species were important, and sometimes exceeded in numbers larvae of burrowing species.

6. Rough estimates of duration of pelagic life and speed of surface water drift show that larvae may be transported considerable distances in the North Sea. Some species showed a southerly movement resembling that of "north-west indicator" species. There was an unusual influx, almost certainly due to water movement, of larvae into the off-Forth region in the autumn of 1949.

7. The month by month distributions of 47 species are given in charts and of 10 species, in addition, in the text.

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#### EXPLANATION OF PLATES VI-VIII.

Charts showing the monthly distribution of types of larvae during 1949. The numbers placed near the observations give the months of occurrence. The scale used to give broad indication of density is given in Plate VI. The dots show those international squares where the corresponding adults were found during quantitative bottom surveys in earlier years. The international squares sampled, and by whom, are shown at the bottom of Plate VIII.

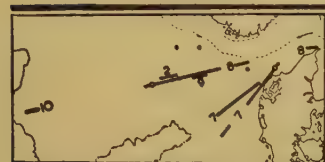


PLATE VI

SCALE

Per mile per block

- ..... + 3
- ..... 4-10
- ..... 11-25
- ..... 26-50
- ..... 51-100
- ..... 101-250
- ..... 251-500



MYTILID A



(PLIMOPSIS)



ADULA SIMPSONI



MODIOLUS MODIOLUS



LIMA



MUSCULUS MARMORATUS



CYPRINA ISLANDICA



ANOMIACEA



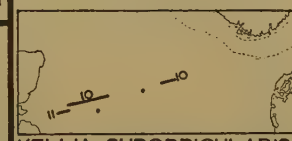
MYRTEA SPINIFERA



"MONTACUTA" 1948



1949

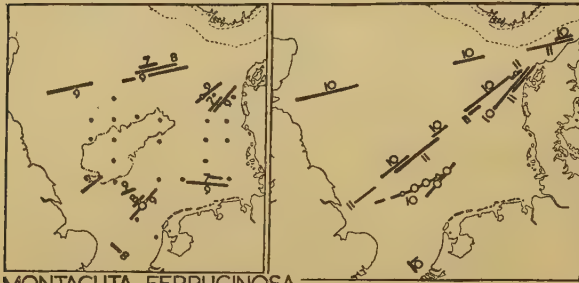


KELLIA SUBORBICULARIS



(PLEPTON SQUAMOSUM)

PLATE VII



MONTACUTA FERRUGINOSA



CARDIUM A



CARDIUM D



VENERID A



(P)PAPHIA



CARDIUM B



VENERID B



VENERIDS C-F



(P)MACRA CORALLINA



MACRID E



(P)PISULA SOLIDA



MAY



OCTOBER



SEPT

(P)DONAX VITTATUS



(P)PISULA ELLIPTICA



(P)PISULA SUBTRUNCATA



(P)TELLINA CRASSA



(P)LUTRARIA LUTRARIA



TELLINA FABULA







# CONTINUOUS PLANKTON RECORDS:

## EXPLANATION AND METHODS, 1946-1949

BY

K. M. RAE, O.B.E., B.Sc.

IN a previous 'Hull Bulletin' Professor Hardy (1941) gave a general introduction to the extended Continuous Plankton Recorder Survey of the North Sea which was started in January, 1938, when University College, Hull, opened their subsidiary laboratory in Leith. Although, due to the outbreak of war, the collection of data was restricted to twenty months, the results obtained from the wider area were encouraging. It was clear that if the work could be continued on such a scale for a number of years it should become possible to obtain a comparatively detailed picture of the changes in quality and quantity of the plankton month by month over the whole North Sea, and by comparing these changes year after year to elucidate some of the underlying causes. There was also the reasonable hope that such an investigation of the distribution and fluctuation in the plankton might throw some light on fishery problems, particularly so if a contemporary but more detailed survey could be made of the plankton on the herring fishing grounds.

Thanks to the continued support of the Development Commissioners and University College, Hull, it was possible to resume the work soon after the end of the war, and when Dr. Lucas reopened the department in May, 1945, he found the owners of the ships and their sea-going and shore personnel as generous in their co-operation as before. At first some unavoidable difficulties were met. Centralization of the shipping administration and the paucity of trade made regular sailing schedules for the merchant ships impossible, and for a time the restriction of all shipping to the channels swept free of mines limited the routes available. However, in January, 1946, S.S. "Spero" of Ellerman's Wilson Line took the first post-war record between Hull and Copenhagen ("C" route), and gradually, route by route, the survey was built up again.

In February, 1946, Messrs. James Currie & Company put the S.S. "Gothland" at our disposal for the Leith to Copenhagen run ("K" route). Two more routes were re-started during June: Aberdeen to Lerwick ("A" route) using the S.S. "St. Clair" of the North of Scotland and Orkney and Shetland Steam Navigation

Company, and Pentland Skerries to Reykjavik ("V" route) using the S.S. "Horsa," which was then on charter to the Icelandic Shipping Company.<sup>1</sup> In September, 1946, the Associated Humber Lines allowed us to use the S.S. "Melrose Abbey" to re-start the Hull to Rotterdam run ("R" route), and almost immediately afterwards they made S.S. "Harrogate" available between Hull and Hamburg ("B" route). In November, 1947, Ellerman's Wilson Line offered their newly commissioned S.S. "Leo" for the London to Skagerrak run ("G" route) which provided an approximation to the pre-war "E" route. As there were no regular sailings from the west coast to Norway and Germany *via* the Pentland Firth ("M" and "Z" routes) or from Leith to Hamburg ("L" route), this appeared to be the closest we could get to the pre-war pattern of the programme. Mention should be made also of two other merchant ships which have also provided valuable assistance, although they have not played a regular part in the routine survey; during the summer and autumn of 1947 the S.S. "St. Clement" of the North of Scotland and Orkney and Shetland Steam Navigation Company provided additional tows between Aberdeen, Stromness and Lerwick ("F" route) for the study of the plankton on the herring fishing grounds, and during the winter of 1947-48 the S.S. "Hebe" of the United Shipping Company, Denmark, took tows from Newcastle and Hull to Danish ports ("N" route). This route was discontinued later because it appeared to be duplicating information already available from other lines.

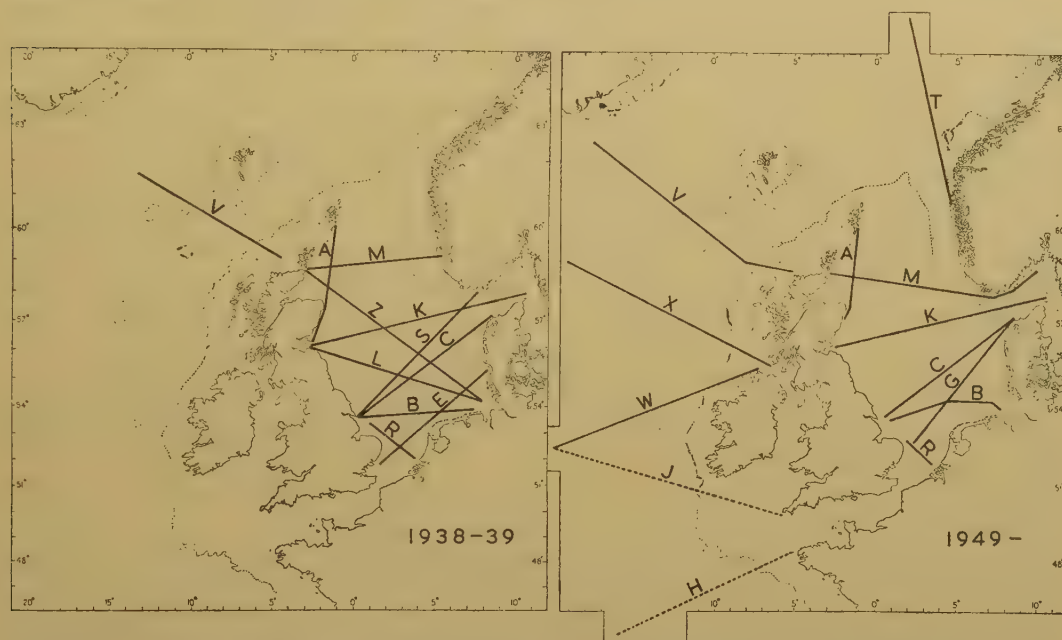
Towards the end of 1947 an excellent opportunity to extend the survey into the Atlantic occurred when the Provisional International Civil Aviation Organization established its ocean weather stations. Stations "Item" and "Jig" at 60°N. 20°W. and 52°30'N. 20°W. respectively became the British responsibility, and four ex-naval corvettes were commissioned to work three week tours of duty sailing from their base at Greenock. It was realized how useful these weather ships might be for collecting hydrographical and biological data in addition to their routine meteorological observations, and it was largely due to Lt.-Cmdr. Lumby of the Ministry of Agriculture and Fisheries and Cmdr. Frankcom of the Air Ministry that we were able to get regular recorder tows to and from these stations from the beginning of their programme. Route "W" to the southern station "Jig" was commenced in November, 1947, and route "X" to the northern station in January, 1948.

Early in 1949 we were able to obtain two valuable additional routes, "M" and "T," thanks to the assistance of Professor Ruud of Oslo University. He introduced us to Messrs. Thor Thoresen of Oslo, who generously agreed to allow us to use S.S. "Sarpfoss." She sails from Manchester through the Pentland Firth to east coast Norwegian ports and so replaces the badly needed pre-war "M"

<sup>1</sup> Early in 1949 the S.S. "Horsa" was returned to her owners to sail in the Leith-Copenhagen trade and regular sailings on the Iceland route were no longer available. However, recently the Directors of the Icelandic Shipping Company were generous enough to offer us facilities of their new passenger ship, the S.S. "Gullfoss," and it was with regret that we discovered that her high cruising speed made her use impracticable.



route. The "Sarpfoss" took her first record in March, 1949, but unfortunately soon afterwards she went out of commission, although now she is in regular service again. Professor Ruud also suggested to the Norwegian Committee responsible for weather station "M" that O.W.S. "Polarfront I" might tow Recorders to and from her station at  $66^{\circ}\text{N}$ .  $02^{\circ}\text{E}$ . Permission was granted and with the help of Professor Mosby and the Geophysical Institute, Bergen, this route "T" was commenced in February, 1949. Each month a loaded Recorder and a spare inside mechanism are shipped to Bergen *via* Newcastle; the inside mechanisms are interchanged while the "Polarfront I" is on station, and when she returns to Bergen the gear is shipped back to the laboratory in Leith.



TEXT-FIG. 1.—Charts showing the standard routes along which the plankton recorder was towed during the 1938-39 survey (left-hand side) compared with those in use during 1949 (right-hand side). Sampling is less regular on routes "J" and "H" than on the others.

For the most recent addition to the programme we are indebted to the Royal Netherlands Meteorological Institute, and also again to Lt.-Cmdr. Lumby, who made the initial arrangements. Under a revised schedule for keeping watches on a reduced number of weather stations the Netherlands weather ship, "Cumulus," became responsible for a number of turns of duty each year on station "J" and station "K" at  $45^{\circ}\text{N}$ .  $16^{\circ}\text{W}$ . Through her assistance we are able to obtain records either along the length of the English Channel or alternatively across the Celtic Sea or south-west into the Bay of Biscay, depending on the station to which she is bound.

It is quite impossible here to give due thanks or acknowledgment to the very

many people whose generous help has enabled us to start and maintain the various Recorder routes which provide our basic data. We are indebted to the captains, officers and crews of the many ships who persevere with the shooting and hauling of the machines, often at considerable inconvenience during inclement weather; without their assistance obviously the work could not continue, and indeed, were they less generous there would be many more gaps in our information. Also much has been done by the shore staffs of the various firms to assist in the despatch and the return of the machines.

Text-fig. 1 shows the recorder routes in operation in 1949 compared with those used in 1938-39. It will be seen that some detail has been lost in the central North Sea due to the absence of the two routes between Scotland and Germany, but the extension into the Atlantic provided by the weather ships in many respects offers compensation for this.

The object, as before, is to obtain one record per month on each route, but a number of factors combine to prevent this ideal being achieved in most months. Inevitably sailing schedules are occasionally upset, and again the worst weather conditions, particularly fog, may preclude the towing of the recorder. Sometimes, as explained by Hardy (1941), a recorder will fail to sample as it should due to some defect, or, alternatively, a suspected defect will cast suspicion on the validity of a particular tow and the results must be discarded. However, thanks to the work of the laboratory staff, these irregularities in working the machine have been reduced to a minimum; something less than 10% of the total mileage sampled is all that need be discarded, and the expected valid sampling in a year amounts to about 30,000 miles.

It became clear soon after we re-started that if the programme was to achieve and maintain its wide scope, and if other lines of research were to be pursued in the department at the same time, some detail of the routine analyses of the recorder results had to be sacrificed. The alternative of taking less frequent records or reducing the number of lines was unattractive. The method of analysis used in the pre-war work has already been outlined by Hardy (1939, p. 36), and described in more detail by the various authors of 'Hull Bulletins,' who explain how it was applied to the various kinds of plankton with which they dealt.

To economize in the time taken over these analyses three changes were adopted in 1946. The first was to dispense with the system of dividing the process into three successive estimations—for phytoplankton, for copepods and for other plankton. It was decided instead to restrict the initial analysis to the identification and quantitative estimation of those species, or where necessary genera or even groups of genera, which could be readily recognized on the silk by the least experienced members of the team. This enables each member of the staff to undertake his share of the routine work and at the same time ensures up-to-date information on the gross changes in the plankton. The records are then stored in their 10-mile units or *blocks* so that workers can return to them and make a more detailed study of any group of plants or animals in which they have particular



interest. The scope of the initial or *routine* analysis and the subsequent or more specialized analyses is outlined in the Appendix below.

A second and very considerable economy in time was effected by the decision to apply the routine analysis to only every alternate 10-mile block. Such a decision was taken with regret, because it meant sacrificing the actual continuity of the records, and at the same time halved the chance of finding the less common forms whose distribution appeared interesting in the earlier work. But nevertheless the sampling is still continuous, and the alternate blocks which are not examined in the *routine* analysis remain available to a worker should he require to make a more detailed study.

The third modification, which was not introduced until March, 1948, was intended to cut down considerably the time taken in assessing the plankton on each block. Instead of counting the various plants and animals, the worker merely estimates the number present by declaring that he saw less than 11, between 11 and 25, between 26 and 50 and so on in categories which grow wider as the numbers increase. Different arbitrary categories are used for the phytoplankton and the zooplankton, and some forms are merely recorded as present. In brief the detail sought is no finer than that used, for example, by Marshall (1948) in illustrating his results from the 1938-39 period of the recorder survey. The system sounds at first more complicated than it really is and, for the reader who may be interested, the details are given in the Appendix with some discussion of the implications. One may say, however, that results obtained by such a method can give a satisfactory picture of the distribution of the plankton, and suprisingly little valid or significant information is lost through not making a more detailed and exact estimate of the contents of a sample which in itself is subject to many random errors.

The initial or *routine* analysis is a compromise between the speed of working and the detail to be obtained ; although restricted in scope it can provide basic information which is useful in a number of ways. The plants and animals estimated are sufficiently varied to allow the continuation of one primary objective of the survey, which is to draw up a type of calendar of the expected plankton changes. It is hoped that by doing this one can postulate a standard sequence of events which will enhance the value of the apparent difference between years, and will at the same time assist in interpreting the more detailed observations taken during research cruises which may be restricted in space and time. The initial analysis can be kept up to date, and so can provide contemporary information about the plankton for other laboratories. It also provides sufficiently accurate data to allow one to show the areas of production of phytoplankton and zooplankton, and to detect boundaries between communities and their movement. Although it offers no information about the more conventional "indicators" such as the species of *Sagitta* and *Thaliacea*, the movements of alternative indicators can be traced, for example the copepods, *Metridia*, *Candacia*, *Rhincalanus*, *Euchaeta* and *Pleuromamma*, the pteropods, *Clio*, *Clione* and *Limacina*, *Tomopteris*, etc.



However, the recorder method of collection really warrants far more detailed analysis. Although the quantity of plankton caught at any one place is small compared with that taken by the usual net haul, it is, in fact, not practicable by any other existing method to obtain such widespread and regular samples. So various workers return to the records to add detail to the initial estimates of certain forms. Dr. Henderson, with assistance from other members of the staff from time to time, has identified the majority of the fish larvae. Mr. Rees, having established identification techniques which are satisfactory even with the mutilated specimens caught by the recorder, has specialized on the distribution of the planktonic larvae of the bottom-living invertebrates, particularly the lamellibranchs, the decapods and the echinoderms, while Mr. Vane has commenced work on the gastropod larvae and more especially the pelagic pteropods. The earlier work of Marshall (1948) on the euphausiids and *Sagitta* has been continued, and to some extent amplified, by Mr. Glover and the writer respectively. Miss John and Miss Jobson are continuing the work on the size-frequency distribution of the phytoplankton which was begun by Dr. Lucas (Lucas and Stubbings, 1948).

These results and those derived from the initial analysis will provide the subject-matter for a number of 'Bulletins' to be published, and much repetition can be avoided if a type of station list is presented here. Detail is not essential; the object being rather to save the individual writer having to define the extent of his available data when discussing the presence or absence of an organism. The charts on Plates IX-XVI show the course and length of the records taken in each month. The arrow-head indicates the direction in which the tow was made and each record is identified by its serial number and route letter. As the samples were all caught at the single depth of 10 metres, it may prove important to differentiate between those taken in daylight and darkness; the periods between sunset and sunrise are indicated by the heavier line. Hardy (1941) has explained the various mechanical defects which may detract from the validity of a particular record. Here, for the sake of simplicity, an arbitrary decision has been made on the validity of each record; the criteria used are essentially the same as before. Those considered to be of quantitative value are shown by solid lines, and those, few in number, which are of doubtful quantitative value but may be used qualitatively to illustrate certain points are shown by broken lines. The dates on which the various tows were taken are given in Table I, together with a *ratio* which expresses the relative speed at which the silk was wound through the machine (see p. 154).

From July to September, 1947, S.S. "Harrogate" traded between Hull and Antwerp ("D" route) instead of between Hull and Hamburg, and so her course lay close to that taken by S.S. "Melrose Abbey" ("R" route). This enabled us to obtain a series of records at much shorter intervals of time than was usually possible. The majority of these extra tows are not drawn on the charts where instead a marginal note of their serial numbers is to be found.

TABLE I.—*A List of the Records shown in Plates IX to XVI Arranged by Months.*

The serial number and code letter of each Record is followed by the date or dates on which the tow was taken. The final figure of each entry gives the ratio of miles per division, *i.e.* the total mileage towed/number of divisions of silk that crossed the water tunnel (see p. 154).

| Record.          | Date. | Ratio. | Record.         | Date.          | Ratio. | Record.      | Date.          | Ratio. |
|------------------|-------|--------|-----------------|----------------|--------|--------------|----------------|--------|
|                  | 1946  |        |                 | 1946 (contd.). |        |              | 1947 (contd.). |        |
| <i>January</i>   |       |        | <i>October</i>  |                |        | <i>March</i> |                |        |
| 86C              | 7/8   | 4.5    | 135R            | 4/5            | 5.5    | 109R         | 2/3            | 5.4    |
|                  |       |        | 35K             | 4/6            | 4.5    | 34A          | 8/9            | 4.6    |
| <i>February</i>  |       |        | 104R            | 6              | 5.4    | 15V          | 9/11           | 5.6    |
| 87C              | 7     | 6.0    | 136B            | 17/18          | 5.4    | 100C         | 22/23          | 5.1    |
| 25K              | 28/1  | 5.1    | 105R            | 18             | 4.9    | 43K          | 22/24          | 4.6    |
|                  |       |        | 11V             | 21/22          | 5.1    |              |                |        |
| <i>March</i>     |       |        | 29A             | 24/25          | 5.6    | <i>April</i> |                |        |
| 88C              | 10/11 | 5.4    | 96C             | 27/29          | 6.1    | 36A          | 8/9            | 4.9    |
| 89C              | 23/24 | 3.6    |                 |                |        | 111R         | 20             | 5.3    |
| 26K              | 29/30 | 5.0    | <i>November</i> |                |        |              |                |        |
|                  |       |        | 106R            | 3              | 4.5    | <i>May</i>   |                |        |
| <i>May</i>       |       |        | 12V             | 14/15          | 4.9    | 112R         | 11             | 5.8    |
| 90C              | 1     | 6.8    | 37K             | 15/17          | 4.9    | 38A          | 17/18          | 4.8    |
| 28K              | 5/6   | 4.5    | 97C             | 20/21          | 5.9    | 101C         | 18/19          | 4.8    |
| 29K              | 29/30 | 4.6    | 30A             | 30/1           | 5.4    | 16V          | 19/20          | 5.4    |
|                  |       |        |                 |                |        | 139B         | 21             | 4.6    |
| <i>June</i>      |       |        | <i>December</i> |                |        | 113R         | 27/28          | 4.6    |
| 21A              | 20/21 | 4.5    | 39K             | 14/16          | 6.0    | 102C         | 28/29          | 5.1    |
|                  |       |        | 31A             | 17/18          | 4.9    |              |                |        |
| <i>July</i>      |       |        | 107R            | 17/18          | 4.3    | <i>June</i>  |                |        |
| 8V               | 8/10  | 5.7    | 98C             | 22/23          | 5.4    | 44K          | 6/8            | 5.0    |
| 92C              | 10    | 5.6    |                 |                |        | 140B         | 10             | 5.2    |
| 31K              | 13/14 | 5.0    |                 |                |        | 39A          | 14/15          | 5.0    |
| 23A              | 27/28 | 4.9    |                 |                |        | 114R         | 24/25          | 4.0    |
|                  |       |        | 1947            |                |        | 103C         | 25/26          | 5.1    |
| <i>August</i>    |       |        | <i>January</i>  |                |        | 115R         | 28/29          | 4.8    |
| 93C              | 4     | 5.2    | 137B            | 2/3            | 5.8    |              |                |        |
| 9V               | 9/10  | 5.4    | 108R            | 12             | 4.0    | <i>July</i>  |                |        |
| 24A              | 17/18 | 4.7    | 99C             | 18/19          | 5.6    | 45K          | 4/6            | 4.8    |
| 33K              | 23/24 | 4.8    | 13V             | 18/19          | 5.6    | 41A          | 5/6            | 4.9    |
|                  |       |        | 32A             | 18/19          | 5.0    | 1D           | 6              | 4.2    |
| <i>September</i> |       |        | 41K             | 24/26          | 5.3    | 42A          | 12/13          | 5.2    |
| 102R             | 1     | 6.3    |                 |                |        | 117R         | 13             | 5.8    |
| 10V              | 1/3   | 5.3    | <i>February</i> |                |        | 2D           | 13             | 4.9    |
| 94C              | 7/8   | 6.2    | 42K             | 7/9            | 5.3    | 104C         | 15/16          | 5.1    |
| 26A              | 14/15 | 5.1    | 14V             | 8/9            | 5.0    | 43A          | 19/20          | 5.0    |
| 34K              | 21/22 | 4.9    | 138B            | 14             | 5.5    | 118R         | 20             | 5.3    |
| 103R             | 22    | 4.6    | 33A             | 16/17          | 6.0    | 17V          | 27/29          | 5.1    |
| 95C              | 28/29 | 5.3    |                 |                |        |              |                |        |

TABLE I.—(contd.)

| Record.          | Date. | Ratio. | Record.         | Date. | Ratio. | Record.        | Date. | Ratio. |
|------------------|-------|--------|-----------------|-------|--------|----------------|-------|--------|
| 1947 (contd.).   |       |        | 1947 (contd.).  |       |        | 1948 (contd.). |       |        |
| <i>August</i>    |       |        | <i>December</i> |       |        | <i>May</i>     |       |        |
| 46K              | 1/2   | 5.0    | 20V             | 4/6   | 4.8    | 111C           | 5/6   | 5.7    |
| 120R             | 5/6   | 6.6    | 109C            | 5/7   | 5.7    | 146B           | 6/7   | 4.9    |
| 3D               | 6     | 4.9    | 130R            | 7     | 4.8    | 55K            | 8/9   | 5.2    |
| 105C             | 6/7   | 5.3    | 3N              | 11/12 | 4.9    | 135R           | 16    | 5.4    |
| 45A              | 9/10  | 4.9    | 50K             | 13/14 | 4.9    | 5W             | 20/21 | 5.6    |
| 121R             | 12/13 | 6.6    | 3G              | 13/14 | 5.2    | 5X             | 22/24 | 6.6    |
| 1F               | 16/19 | 5.2    | 51A             | 16/17 | 4.9    | 7G             | 23/24 | 5.5    |
| 122R             | 17/18 | 6.6    | 2W              | 18/19 | 5.8    | 23V            | 23/25 | 5.1    |
| 123R             | 26/27 | 7.1    |                 |       |        | 112C           | 25/27 | 5.6    |
| 47K              | 29/31 | 4.9    |                 |       |        | 56A            | 29/30 | 6.0    |
| 124R             | 31    | 6.1    |                 |       |        |                |       |        |
|                  |       |        | 1948            |       |        | <i>June</i>    |       |        |
| <i>September</i> |       |        | <i>January</i>  |       |        | 56K            | 5/6   | 5.5    |
| 18V              | 2     | 5.0    | 21V             | 7/9   | 5.9    | 147V           | 5/6   | 5.6    |
| 4D               | 3     | 5.3    | 52A             | 15/16 | 4.9    | 24V            | 10/12 | 4.8    |
| 106C             | 2/4   | 4.9    | 51K             | 16/18 | 5.1    | 6W             | 12/13 | 5.4    |
| 47A              | 6/7   | 5.2    | 1X              | 16/19 | 5.4    | 136R           | 13    | 4.9    |
| 2F               | 7     | 5.2    | 4G              | 22/23 | 5.5    | 6X             | 14/15 | 5.1    |
| 5D               | 14    | 5.4    | 131R            | 25    | 5.4    | 113C           | 16/17 | 5.7    |
| 125R             | 21    | 6.6    | <i>February</i> |       |        | 57A            | 19/20 | 5.1    |
| 141B             | 24/25 | 5.6    | 2X              | 4/6   | 5.0    | <i>July</i>    |       |        |
| 126R             | 28    | 5.1    | 52K             | 13/15 | 4.9    | 7W             | 1/3   | 6.2    |
| <i>October</i>   |       |        | 132R            | 15    | 5.0    | 57K            | 3/4   | 6.0    |
| 48K              | 11/12 | 5.2    | 53A             | 16/17 | 4.8    | 58A            | 3/4   | 6.1    |
| 127R             | 11/12 | 4.6    | 22V             | 19/20 | 4.6    | 114C           | 6/7   | 5.7    |
| 49A              | 18/19 | 4.6    | 3W              | 24/25 | 6.6    | 59A            | 10/11 | 4.8    |
| 3F               | 21    | 6.1    | 5G              | 25/26 | 5.0    | 137R           | 11    | 4.6    |
| 107C             | 24/26 | 6.0    | <i>March</i>    |       |        | 8G             | 19/20 | 4.6    |
| 142B             | 25/26 | 9.7    | 5N              | 12/13 | 6.6    | 60A            | 24/25 | 6.5    |
| 128R             | 28/29 | 6.4    | 144B            | 19/20 | 5.4    | 7X             | 24/26 | 5.6    |
| <i>November</i>  |       |        | 4F              | 19/20 | 4.9    | 148B           | 30    | 5.3    |
| 19V              | 1/3   | 5.2    | 54A             | 23/24 | 5.8    | <i>August</i>  |       |        |
| 143B             | 7/8   | 5.7    | 53K             | 26/28 | 4.7    | 58K            | 30/1  | 4.7    |
| 49K              | 7/9   | 5.1    | 133R            | 28    | 5.2    | 25V            | 1/3   | 5.5    |
| 129R             | 9     | 5.2    | 6G              | 29/30 | 4.6    | 62A            | 7/8   | 5.5    |
| 1G               | 9/10  | 5.2    | <i>April</i>    |       |        | 115C           | 9/10  | 5.8    |
| 108C             | 12/14 | 6.5    | 145B            | 6/7   | 5.0    | 9X             | 12/14 | 7.1    |
| 1N               | 20/21 | 5.4    | 4W              | 7/9   | 7.4    | 8W             | 12/14 | 6.7    |
| 50A              | 22/23 | 4.9    | 54K             | 9/11  | 5.0    | 149B           | 14    | 5.3    |
| 1W               | 22/24 | 5.4    | 3X              | 11/13 | 5.0    | 63A            | 14/15 | 5.1    |
| 2G               | 29    | 5.3    | 110C            | 14/15 | 5.5    | 138R           | 14/15 | 5.1    |
| 2N               | 30    | 5.3    | 55A             | 17/18 | 5.6    | 9G             | 16/17 | 4.7    |
|                  |       |        | 134R            | 25    | 4.6    | 64A            | 21/22 | 5.6    |
|                  |       |        |                 |       |        | 59K            | 27/29 | 4.6    |



TABLE I.—(contd.)

| Record.          | Date. | Ratio. | Record.         | Date. | Ratio. | Record.           | Date.   | Ratio. |
|------------------|-------|--------|-----------------|-------|--------|-------------------|---------|--------|
| 1948 (contd.).   |       |        | 1949            |       |        | 1949              |         |        |
| <i>September</i> |       |        | <i>January</i>  |       |        | <i>May contd.</i> |         |        |
| 9W               | 4/6   | 6.0    | 64K             | 1/3   | 5.7    | 22X               | 14/16   | 6.0    |
| 26V              | 6/7   | 6.3    | 16X             | 8/10  | 5.4    | 128C              | 18/19   | 5.2    |
| 116C             | 8/9   | 6.0    | 122C            | 12/13 | 4.8    | 157B              | 26/27   | 4.7    |
| 65A              | 11/12 | 5.4    | 15G             | 14/15 | 5.6    | 72A               | 28/29   | 6.0    |
| 139R             | 12    | 5.3    | 147R            | 23    | 4.0    | 4T                | 30/31   | 6.5    |
| 10G              | 14/15 | 4.7    | 17X             | 27/29 | 11.1   |                   |         |        |
| 11X              | 23/25 | 5.8    | 1T              | 27/29 | 5.7    |                   |         |        |
| 60K              | 24/26 | 4.9    |                 |       |        | <i>June</i>       |         |        |
| 11G              | 25/26 | 4.9    | <i>February</i> |       |        | 21W               | 2/4     | 6.0    |
| 117C             | 29/30 | 5.9    | 123C            | 1/3   | 4.6    | 23X               | 2/3 & 9 | 6.0    |
|                  |       |        | 154B            | 4/5   | 4.5    | 72K               | 3/5     | 5.8    |
| <i>October</i>   |       |        | 67K             | 11/12 | 5.6    | 151R              | 19      | 5.5    |
| 150B             | 7     | 4.6    | 18X             | 18/20 | 6.8    | 73A               | 25/26   | 6.2    |
| 140R             | 10    | 4.8    | 16W             | 20    | 5.4    | 24X               | 25/27   | 5.9    |
| 12X              | 15/17 | 6.4    | 124C            | 23/24 | 6.0    | 130C              | 28/30   | 4.4    |
| 66A              | 16/17 | 5.4    | 69A             | 24/25 | 5.4    |                   |         |        |
| 27V              | 16/18 | 6.7    |                 |       |        | <i>July</i>       |         |        |
| 118C             | 19/21 | 5.3    | <i>March</i>    |       |        | 19G               | 1/2     | 5.1    |
| 151B             | 21/22 | 5.3    | 17W             | 9/11  | 6.9    | 23W               | 14/16   | 6.1    |
| 61K              | 22/24 | 5.2    | 19X             | 10/12 | 7.2    | 158B              | 15      | 5.0    |
| 142R             | 26/27 | 5.5    | 16G             | 11/12 | 4.3    | 73K               | 15/17   | 4.4    |
| 152B             | 28/29 | 5.9    | 68K             | 12/13 | 4.9    | 74A               | 16/17   | 5.8    |
|                  |       |        | 148R            | 13    | 5.3    | 152R              | 17      | 5.9    |
| <i>November</i>  |       |        | 125C            | 15/17 | 6.6    | 131C              | 20/21   | 4.4    |
| 11W              | 5/6   | 6.3    | 30M             | 18/20 | 6.6    |                   |         |        |
| 13X              | 5/7   | 6.3    | 70A             | 19/20 | 6.1    | <i>August</i>     |         |        |
| 119C             | 10/11 | 4.8    | 2T              | 30/1  | 7.3    | 159B              | 5       | 5.4    |
| 12G              | 12/13 | 5.2    |                 |       |        | 74K               | 6/7     | 5.5    |
| 62K              | 19/21 | 4.9    | <i>April</i>    |       |        | 26X               | 6/8     | 5.8    |
| 13G              | 20/21 | 4.8    | 18W             | 1/3   | 6.1    | 24W               | 7/8     | 5.4    |
| 144R             | 21    | 6.3    | 20X             | 2/4   | 6.3    | 75A               | 13/14   | 5.5    |
| 28V              | 24/26 | 6.1    | 126C            | 6/7   | 6.1    | 153R              | 14      | 5.8    |
| 12W              | 27/28 | 6.7    | 149R            | 17    | 5.1    | 20G               | 17/18   | 5.1    |
| 14X              | 27/29 | 5.4    | 21X             | 20/23 | 6.6    | 25W               | 25/27   | 6.4    |
| 67A              | 30/1  | 6.2    | 19W             | 21/23 | 6.6    | 27X               | 25/27   | 7.3    |
|                  |       |        | 155B            | 23/24 | 4.7    | 133C              | 31/1    | 5.4    |
| <i>December</i>  |       |        | 17G             | 26/27 | 4.9    |                   |         |        |
| 120C             | 3/1   | 4.8    | 127C            | 26/28 | 4.6    | <i>September</i>  |         |        |
| 15X              | 16/18 | 5.4    | 156B            | 28/29 | 4.9    | 7T                | 31/2    | 5.8    |
| 13W              | 16/18 | 7.2    | 3T              | 30/2  | 5.1    | 160B              | 10      | 4.9    |
| 63K              | 17/19 | 4.7    |                 |       |        | 76A               | 10/11   | 5.8    |
| 68A              | 18/19 | 4.9    | <i>May</i>      |       |        | 21G               | 12/13   | 4.8    |
| 145R             | 19    | 5.3    | 71A             | 7/8   | 6.5    | 26W               | 17/18   | 5.7    |
| 14G              | 19/20 | 4.5    | 150R            | 7/8   | 5.1    | 28X               | 17/19   | 7.6    |
| 121C             | 22/23 | 4.7    | 20W             | 14/15 | 5.4    | 134C              | 20/22   | 4.9    |
| 153B             | 26/27 | 4.8    |                 |       |        | 155R              | 25      | 5.0    |
|                  |       |        |                 |       |        | 75K               | 25/26   | 6.0    |

TABLE I.—(contd.)

| Record.        | Date. | Ratio. | Record.         | Date. | Ratio. | Record.         | Date. | Ratio. |
|----------------|-------|--------|-----------------|-------|--------|-----------------|-------|--------|
|                | 1949  |        |                 | 1949  |        |                 | 1949  |        |
| <i>October</i> |       |        | <i>November</i> |       |        | <i>December</i> |       |        |
| 27W            | 5/6   | 6.2    | 136C            | 2/3   | 5.6    | 30W             | 11/12 | 5.2    |
| 29X            | 6/8   | 8.6    | 77K             | 4/6   | 6.2    | 32X             | 11/13 | 5.7    |
| 76K            | 7/9   | 5.6    | 23G             | 9/10  | 5.7    | 138C            | 14/15 | 5.2    |
| 161B           | 8     | 4.8    | 78A             | 12/13 | 5.0    | 78K             | 18/21 | 5.6    |
| 135C           | 11/13 | 6.2    | 29W             | 16/19 | 6.1    | 79A             | 20/21 | 4.7    |
| 22G            | 12/13 | 5.1    | 31X             | 17/18 | 6.2    | 9T              | 27/28 | 6.3    |
| 156R           | 16    | 5.5    | 157R            | 20    | 5.2    | 31W             | 30/31 | 7.7    |
| 77A            | 22/23 | 5.0    |                 |       |        | 33X             | 30/1  | 5.2    |
| 28W            | 25/26 | 5.2    |                 |       |        |                 |       |        |
| 8T             | 29/30 | 6.9    |                 |       |        |                 |       |        |
| 30X            | 30/1  | 6.5    |                 |       |        |                 |       |        |

## APPENDIX.

If one wishes to consider the usefulness of a plankton sample as a measure of the plankton present in the sea, it is convenient to divide the potential sources of error into two categories. First one must decide how good an estimate of the plankton the sample collected can give and, secondly, how accurate is the estimate of the contents of the sample made in the laboratory. The errors in the first category are, in the main, uncontrollable within a particular experiment. They are intrinsic to the method of collection and the manner in which the plankton is distributed in the sea at the time of collection; they may be extremely difficult to evaluate. Whereas those in the second category are strictly controllable, almost to the extent of elimination, if the total content of the sample is counted. There is, however, reason to suppose that in most methods used for plankton sampling misleading information will arise far more often from the failure of the sample to be typical of the population than from the inadequacy of the subsequent estimate of the contents of the sample. There is evidence that when all sources of error are combined only differences of the order of  $\times \frac{1}{2}$  or  $\times 2$  for vertical hauls and  $\times \frac{1}{4}$  or  $\times 4$  for horizontal hauls may be considered significant.<sup>1</sup> The estimate of the plankton in the immediate area of the sample can be improved by replicate hauls, but nevertheless, if the results are to be interpreted in any useful way, it is necessary to postulate smooth density gradients between those stations, or hauls, which are considered to be significantly different. This may well be a dangerous assumption if the observations are widely spread in space or in time. Distances of 10 or 20 miles between stations must be expected even in an intensive survey of a comparatively restricted area if nets are to be used, while even more serious is the usual time interval of a month or more between each

<sup>1</sup> Winsor and Clarke (1940) estimate coefficients of variation as high as 45% for vertical hauls taken as close together as is practically possible and of the order of 100% for half hour horizontal hauls taken with 12 cm. nets 2 metres apart. Barnes (1951) shows comparable figures for 10 minute horizontal hauls taken with two Hardy Plankton Indicators from the same boat.

series of samples if one considers the extent of the development and the decline in the population which may occur during such a period.

As has been pointed out (Hardy, 1941), the recorder has an inherent advantage over other conventional plankton methods in that the samples it takes are continuous along the course of a tow, and so there is no necessity to interpolate between observations in this dimension. The horizontal tow can be divided into units or samples of any length but, as a result of its continuity, the minor variations in density of the plankton along the route will be smoothed out and averaged automatically over whatever length of tow is considered. This advantage is offset to some extent by the fact that samples are all taken at a single depth—10 metres—which may not give a representative picture of the whole water column, although there is evidence that for many planktonic forms it provides a good average value in shallow water (Lucas, 1940 ; Rae and Fraser, 1941).

Unfortunately it has not yet been possible to assess the order of experimental error which may be expected for the recorder as a sampling device. There are practical difficulties in obtaining the necessary number of parallel tows for statistical analysis.<sup>1</sup> But even if there were sufficient data for an analysis of variance there would remain, as a limitation of an estimate of the residual experimental error, the fact that it was only applicable to the particular set of circumstances prevailing when the data were obtained. This is a very real difficulty present in all attempts to assess the validity of samples taken from the sea, regardless of the collecting equipment under test. Because of the enormous variations in population densities, the different rates of change of population level for different organisms, different behaviour and habit between species, changing habits with local conditions or with seasons, etc., it will be necessary to have a vast number of experiments and independent estimates of variance before useful significance levels can be found for differences between hauls which can be generally used.

In the recorder work, although no hard and fast rule has been adopted, an arbitrary criterion of about  $\times 3$  has been taken as being indicative of a significant difference between observations, but it should be stressed that there is no statistical backing for such a criterion, only loose analogy with the statistical analyses of other types of sampling. Fortunately, however, seldom if ever is it necessary to imply differences between pairs of observations in the recorder work because there are so many data available at any one time. The type of differences in population density which were considered significant in the earlier work were not only large, but were evident from a number of successive samples which lent sufficient confidence to the conclusion that there was, in fact, a real difference. In the early stages of the work there was something to be gained by attempting

<sup>1</sup> Preliminary tests have been made from the vessels of the Fishery Protection Flotilla, H.M.S. "Mariner" and H.M.S. "Welcome," and recently Dr. Barnes of the Marine Station, Millport, has obtained duplicate records from F.R.V. "Calanus." An attempt has been made to obtain regular parallel tows from the S.S. "Gothland" on the Leith-Copenhagen route, but this led to the loss of a recorder and it had to be discontinued. Dr. Barnes hopes to obtain further results in the near future when more Recorders can be made available.



maximum accuracy in the analysis of the sample content to determine the frequency with which catches of various sizes were taken. But this achieved, it was plain that as no fine limits of accuracy could be placed on the sample as a measure of the population from which it was taken, much unwarranted time might be spent in making an unnecessarily detailed estimate of its contents. The type of differences sought and, from past experience expected to be found, would be apparent even if only approximate estimates were made. So a compromise between the time spent on the analysis of each sample and the detail required was adopted.

It was found that a worker, having made a traverse with a microscope, could, after practice, easily declare what order of numbers of any organism was included in the traverse, and could do this much faster, as one would expect, than he could actually count each organism. Working on this premise a schedule for the *routine* analysis was developed. It may be wise to describe this schedule in some detail to save repetition in subsequent 'Bulletins,' in which the implication of the results may be very dependent on the method used in estimating the plankton. Also as other laboratories commence to use the recorder technique an account of our tried method may be useful.

During 1946 and 1947 the method was effectively the same as that used in the pre-war work, except that it was only applied to alternate blocks. The method outlined below was generally adopted in March, 1948.

The *routine* analysis can be conveniently divided into three successive stages :

#### 1. *Colour Analysis.*

As soon as the recorder is returned to the laboratory the silk is unwound and a visual assessment is made of the quality of the plankton caught. The main purpose is to obtain an impression of the quantity and extent of the phytoplankton. Those 2 inch divisions of silk which are coloured green are compared with a standard but arbitrary colour scale and categorised as "very pale green," "pale green," "green" and "very green." When dinoflagellates are present in numbers a characteristic green brown tinge is recognizable and is recorded. At the same time notes are made about obvious patches of zooplankton and the presence or absence of the reddish colour which is variably present in the copepods.

The silk is next cut into lengths each representing 10 miles of tow and each length or block is given a serial number starting from the end nearest the home port. The 10-mile samples are then divided into those with odd serial numbers, "*odd blocks*," and those with even, "*even blocks*." The "*even blocks*" are put on one side and the "*odd blocks*" only are submitted to analysis as below.

#### 2. *Naked Eye Counts.*

The larger organisms present on the silk are counted or estimated with the naked eye. If 1, 2 or 3 are present the actual number is recorded, but if more are on the silk the worker estimates in which of a series of categories the number falls. These categories are as follow :

| Category.             | Number accepted as<br>being present<br>(see p. 151 below). |
|-----------------------|------------------------------------------------------------|
| 1, 2, 3 actual counts | 1, 2, 3                                                    |
| 4 to 11 estimate      | 6                                                          |
| 12 to 25    ,,        | 17                                                         |
| 26 to 50    ,,        | 34                                                         |
| 51 to 125   ,,        | 75                                                         |
| 126 to 250   ,,       | 160                                                        |
| 251 to 500   ,,       | 320                                                        |
| etc.                  | etc.                                                       |

The groups of animals treated in this way and the degree of identification undertaken are as follows :

COPEPODA.—All individuals as large or larger than the Vth copepodid stage of *Metridia lucens* to species.<sup>1</sup>

AMPHIPODS.—In three groups—caprellids, gammarids and hyperiids.

DECAPOD larvae.—A single group including the zooae and megalopae but excluding the schizopod stages : see below.

SCHIZOPODS.—A combined group containing the schizopod stages of the decapods, stomatopod larvae, all stages of mysids and euphausiids.

PTEROPODS.—Limacina larger than 3 meshes of silk (about 1 mm.) and all others to genus.

CHAETOGNATHS.—All over 1 cm. in length combined.

THALIACEA.—Salps and doliolids combined.

FISH LARVAE.—All combined.

FISH EGGS.—All combined but differentiation made between those > 3 meshes and < 3 meshes of silk.

If in the opinion of the worker any of these forms are too abundant to be fairly estimated with the naked eye, he may elect to enter the number estimated by the microscope traverse : see below.

### 3. *Phytoplankton Fields.*

The phytoplankton is estimated by viewing a known fraction of the silk with a microscope using a  $\frac{1}{2}$  in. objective and  $\times 6$  eye-piece or a  $\frac{2}{3}$  in. objective and a  $\times 10$  in. eyepiece, either of which give the same size of field with the equipment used. Five fields are examined on both the filtering and covering silk (or on the filtering silk only if cellophane has been used—see Hardy, 1939, p. 26). The frac-

<sup>1</sup> The copepodid stages of *Euchaeta* and *Pleuromamma* may be difficult to identify specifically when they are crushed or mutilated, and in such cases the genus only is recorded.

tion so examined is approximately  $\frac{1}{1400}$  of the total area of silk. Again the worker merely declares the order of the numbers of any particular diatom seen :

| Estimated number<br>in 10 (5) fields. | Approximate range<br>of cells present on<br>the silk. | Recorded as— |
|---------------------------------------|-------------------------------------------------------|--------------|
| 1 - 5 .                               | 7,000 .                                               | +            |
| 6 - 50 .                              | 7,000 - 70,000 .                                      | ++           |
| 51 - 500 .                            | 70,000 - 700,000 .                                    | +++          |
| 501 - 5,000 .                         | 700,000 - 7,000,000 .                                 | ++++         |
| etc.                                  | etc.                                                  | etc.         |

If, however, a single cell of any diatom or dinoflagellate included in the types identified is seen at any stage in the analysis its presence is recorded in the lowest category by +.

Cells of only the following are selected for identification :

Rhizosolenia—all species (including the varieties of *R. styliiformia* and *R. alata*), excepting *R. faeroense*, *R. delicatula* and *R. frahillima*, which are included in the category "other diatoms."

Biddulphia—*B. sinensis*, *B. regia*, *B. alternans*, and *B. aurita*.

Thalassiothrix—*Thx. longissima* and *Thx. nitzschoides*.

Thalassiosira (including Coscinosira)—as a combined group.

Coscinodiscus—*C. concinnus* only.

Chaetoceros—Divided into the sub-groups, phaeocerids and hyalochaetes.

Asterionella—to genus.

Eucampia—to genus.

Bacillaria—to genus.

Dactyliosolen—*D. mediterraneus* and *D. antarcticus*.

*Paralia sulcata*—(number of chains estimated).

*Bellaroehia malleus*—(number of chains estimated).

*Guinardia flaccida*—(number of chains estimated).

Nitzschia—*N. seriata* only.

"Other Diatoms"—A category which includes all diatom cells not listed above. Notes are made regarding the predominant genera or species in this category.

Ceratium—to species.

Prorocentrum—to genus.

Dinophysis—to genus.

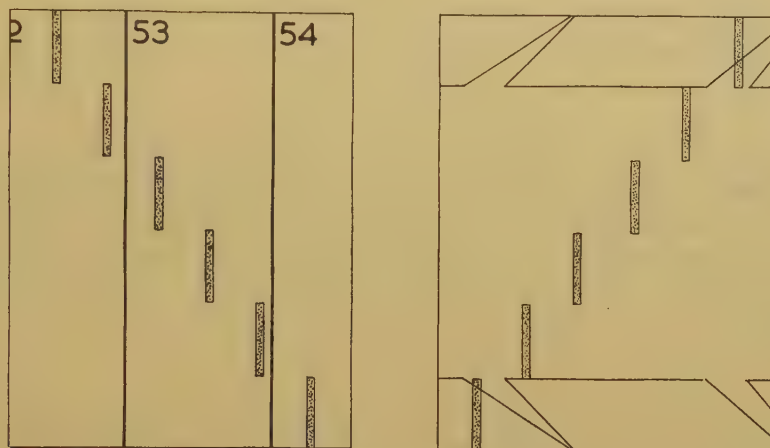
Peridinium (including Gonialax etc.)—as a combined group.

"Total Ceratia"—A category summing all Ceratia and including those already estimated above.



#### 4. Zooplankton Traverse.

A staggered microscope traverse (see Text-fig. 2) is taken across the filtering and covering silks (or filtering silk only if cellophane is used) using a  $\frac{2}{3}$  in. objective and a  $\times 6$  eyepiece. Such a traverse includes in its field approximately  $\frac{1}{40}$  of the total area of silk if the 10-mile block is 4 in. long, though the fraction may be increased or decreased if the ratio differs from 5 miles per 2 in. division of silk.



TEXT-FIG. 2.—A 10-mile block as it appears when the covering silk has been turned back from the filtering silk ready for analysis. The filtering silk, marked off into 2-inch divisions is shown on the left and the covering silk with its folded edges is on the right. That part of the silk which is included in the microscope field during the *staggered* traverse used for estimating the zooplankton is represented by the dotted areas.

Certain organisms seen during the course of this traverse are merely recorded as being present regardless of their abundance. These are: Halosphaera, Silicoflagellata, Foraminifera, Radiolaria, cirripede larvae, polychaete larvae, echinoderm post-larvae, copepod eggs, other eggs and cysts combined, etc.; other objects such as faecal pellets, etc. are recorded in the same manner.

Other animals which are estimated comprise :

- Limacina and other gastropod larvae combined if  $< 3$  meshes of silk.
- Lamellibranch larvae combined.
- Echinoderm larvae combined.
- Cyphonautes larvae combined.
- Cladocera—Podon and Evadne combined.
- Appendicularia—all species combined.
- Chaetognaths—all species  $< 1$  cm. in length combined.

The estimated numbers seen are placed in the following categories ;

| (a)                                             |   | (b)                                                                |   | (c)                                                   |
|-------------------------------------------------|---|--------------------------------------------------------------------|---|-------------------------------------------------------|
| Estimated<br>number<br>seen in the<br>traverse. |   | Approximate range<br>of number present<br>on silk (10-mile block). |   | Number accepted<br>as being present.<br>(see p .151). |
| 1 - 11                                          | . | 40 - 440                                                           | . | 140                                                   |
| 12 - 25                                         | . | 480 - 1,000                                                        | . | 700                                                   |
| 26 - 50                                         | . | 1,040 - 2,000                                                      | . | 1,350                                                 |
| 51 - 125                                        | . | 2,040 - 6,000                                                      | . | 3,000                                                 |
| 126 - 250                                       | . | 6,040 - 10,000                                                     | . | 6,500                                                 |
| 251 - 500                                       | . | 10,040 - 20,000                                                    | . | 13,000                                                |
| etc.                                            |   | etc.                                                               |   | etc.                                                  |

At the same time the smaller copepods (*i.e.*, smaller than *M. lucens* Stage V) are identified and estimated, and a supplementary estimate is made if necessary of the animals already counted with the naked eye (paragraph 2 above), and for this purpose the same numerical categories are used except at the lower end of the scale, less than 12 seen, where there is added detail. So that columns *a*, *b* and *c* above read :

| (a)    |   | (b)       |   | (c)  |
|--------|---|-----------|---|------|
| 1      | . | 40        | . | 40   |
| 2      | . | 80        | . | 80   |
| 3      | . | 120       | . | 120  |
| 4 - 11 | . | 160 - 440 | . | 240  |
| etc.   |   | etc.      |   | etc. |

The degree of identification used for the copepods is that described in Bulletin 14 (Rae and Rees, 1947) :

All Calanoids to species, except *Acartia* to genus only, and the combined group, *Pseudocalanus*, *Microcalanus* and *Paracalanus*.

Cyclopoids—*Corycaeus* and *Oithona* to genus ; other cyclopoids combined.

Harpacticoids—all combined.

An estimate of the " Total copepoda "—*i.e.*, all species combined.

To ensure that an individual worker does not develop idiosyncrasies in estimation or that the criteria he uses do not change, a record is always divided between workers for analysis. Consistent differences rarely occur, but as and when they do they are easily detected.

The methods used for the subsequent and more detailed analyses of certain forms such as the fish larvae, the euphausiids, *Sagitta*, lamellibranch larvae, etc., have varied to suit the particular purpose. They will be described by the individual workers concerned,

Such a system of estimating the catch may be satisfactory for the purpose of charting the results to obtain an overall impression of the distribution of an organism in the manner adopted in earlier Bulletins, but if one is to sum or average observations, it becomes necessary to postulate a finite value for each numerical category. A theoretical consideration of the expected frequency distribution of numbers within a category is complicated. Considering the whole range of numbers found, as a first premise, one might expect *Poisson* distributions to emerge from the sampling technique, but clearly the mean or variance of these will depend on the population density, and so may vary both in time and between species. So one might expect an approximation to some negative binomial to result from summing the *Poisson* type frequency distributions over an extended period, although the characteristics of the expansion would not necessarily be the same for different species which had different mean population levels. A further complication arises through the probability of considerable population gradients in such a wide area at any one time. In fact, a detailed statistical study of the frequency with which catches of various size occur in the extensive data available might well be of interest, but it is beyond the scope of an introduction. For the present purpose an empirical method provides the simplest and most practical approach, although to the more mathematically minded reader it may appear over-elementary.

By returning to the data obtained in the earlier years of the survey when numbers of organisms were estimated to the nearest multiple of a factor (varying, from 10 to 45), or were counted exactly in the cases of the larger and less abundant forms, it is possible to determine the frequency with which any sample size occurred. The information required is conveniently set out in the plates in Rae and Rees (1947); on these charts some species are plotted to the nearest 100 individuals per block, while *Calanus* VI and V are shown to the nearest 10 per block. All that need be done is to count or plot the frequency of occurrence of the various numerals which would have fallen in the categories now in use, and then to calculate their mean for each category. Table II shows a series of these computed means, the number of samples on which each calculation was based and the arbitrary value accepted for the current work.

TABLE II.

| Range or category. | Mean value based on— |                      |                     |                     | Accepted mean. |
|--------------------|----------------------|----------------------|---------------------|---------------------|----------------|
|                    | Calanus V and VI.    | Total copepods.      | Pseudo-calanus.     | Acartia.            |                |
| 160-440            | 240 <sup>68</sup>    | —                    | —                   | —                   | 240            |
| 480-1,000          | —                    | 700 <sup>962</sup>   | 685 <sup>601</sup>  | 695 <sup>83</sup>   | 700            |
| 1,040-2,000        | —                    | 1,400 <sup>740</sup> | 1,340 <sup>86</sup> | 1,350 <sup>55</sup> | 1,350          |
| 2,040-5,000        | —                    | 2,900 <sup>492</sup> | 3,000 <sup>82</sup> | 3,050 <sup>25</sup> | 3,000          |
| 5,040-10,000       | —                    | 6,400 <sup>101</sup> | —                   | —                   | 6,500          |



Next one can attempt to assess the usefulness of these *accepted means* for computation and what order of accuracy can be expected from them. *Coefficients of variation* have been calculated for each category on the basis of the mean square difference from the *accepted mean* and these are shown in Table III. But there may be doubt as to how they can be applied to skew frequency distributions in which the maximum negative error is, in fact, the commonest single occurrence and in which individual positive errors can be three times as great as the largest negative ones, although the expectancy of their occurrences is correspondingly less. Clearly the position could be improved by some drastic transformation, but, as will be seen from Table II, there are sufficient observations available in each category to allow an empirical estimate to be made of the frequency with which errors exceeding any value occurred in the past or may be expected to occur in the future. Selected limits of accuracy are also shown in Table III, using the observed figures for *Calanus* V and VI in the lowest category and the total copepods in the others.

TABLE III.

| Accepted mean. |                    | Standard error. | Coefficient of variation. | Percentage of observations which differ from the accepted mean by more than— |      |        |
|----------------|--------------------|-----------------|---------------------------|------------------------------------------------------------------------------|------|--------|
|                |                    |                 |                           | $\frac{1}{2}$ S.E.                                                           | S.E. | 2 S.E. |
| 240            | Calanus V and VI . | 60              | 25%                       | 81                                                                           | 38   | 13     |
| 700            | { Total Copepods . | 185             | 26%                       | 83                                                                           | 47   | 12     |
|                | { Pseudocalanus .  | 170             | 24%                       | 84                                                                           | 48   | 12     |
|                | { Acartia .        | 155             | 22%                       | 80                                                                           | 40   | 9      |
| 1350           | { Total Copepods . | 320             | 24%                       | 79                                                                           | 40   | 6      |
|                | { Pseudocalanus .  | 290             | 21%                       | 86                                                                           | 38   | 2      |
|                | { Acartia .        | 300             | 22%                       | 80                                                                           | 35   | 8      |
| 3000           | { Total Copepods . | 830             | 28%                       | 70                                                                           | 33   | 5      |
|                | { Pseudocalanus .  | 960             | 32%                       | 78                                                                           | 28   | 3      |
|                | { Acartia .        | 930             | 31%                       | 72                                                                           | 28   | 8      |
| 65000          | Total Copepods .   | 1240            | 19%                       | 67                                                                           | 33   | 5      |

As one would anticipate, the incidence of errors of any given size is considerably greater than in the more familiar case in which the errors conform to a normal distribution. Nevertheless, if one wishes to average, or sum, a number of observations which have been given the *accepted value* for a category, the figures in Table III can provide an idea of the accuracy which can reasonably be attributed

to the result. Regardless of the skew distribution, it is true to say that the standard error of the average or sum will approximate to the standard error of a single observation divided by the square root of the number of observations used in computing the average. In practice, if the intention is to find a value for the mean population density of an organism on any recorder line or in any month by averaging all available observations, it will be found that little accuracy has been lost through using these arbitrary categories instead of finite estimates; this point will be demonstrated in detail as the need arises in the 'Bulletins' that will follow.

Further, to raise a point which is indeed obvious, we have only considered above the loss of detail entailed in the laboratory, in estimating the content of the sample and not the sum of the errors in estimating the population from which the sample was taken. In fact, the detail lost will be small when considered against the total errors involved in the recorder method or most other sampling techniques used in plankton work.

There is, however, a drawback arising from this use of categories in estimating the number of animals caught which can become noticeable if the method of charting the results similar to that used in the pre-war 'Bulletins' is adopted. It introduces a type of error which is most unlikely to influence any conclusions drawn from the results, but nevertheless, it may be mentioned in case anyone wishes to place an unwarranted degree of significance on the published figures. Here it has been presupposed that two divisions of filtering silk pass through the recorder during each ten miles of tow, or alternatively that the area of silk representing ten miles of tow, is 40 times that examined in one traverse with the microscope. For example, when the worker has seen any number of copepods between 12 and 25 in the traverse, it has been declared that between 480 and 1000 were present on the silk and the arbitrary mean value of 700 has been accepted. If, however, the silk had actually wound slower and, say, only  $1\frac{1}{2}$  divisions of silk had represented ten miles of tow, the correct factor would have been 30 and the correct limits 360 to 750 with a mean at about 525. Unfortunately the ratios of silk to mileage have not been consistent during recent years. This, it should be explained, is not due to any intrinsic limitation of the recorder, but to a short-sightedness in planning the recent work for which the writer must accept responsibility. In the pre-war years, and in 1946 and 1947, a factor by which the traverse count should be raised to give the number of organism per 10-mile *block* was calculated for each record and it should have been realized how necessary it would become to keep this factor as constant as possible when the new system of estimating was adopted in March, 1948. This important point was overlooked, and there has been a tendency to reduce the speed of winding for two reasons; it led to economy in the use of silk, which has become progressively more expensive and more difficult to import from Switzerland, and also it permitted the maximum length of tow on the Atlantic lines without the risk of the silk running right through. The situation is aggravated by the fact that there has been a tendency for the

higher ratios or lower factors to occur on the Atlantic lines. There is included in Table I for every record the ratio of the mileage towed to the number of 2-inch divisions of filtering silk which crossed the water tunnel, or in other words the mileage represented by each 2-inch division of silk. When this ratio is 5.0, or exactly two divisions of silk comprise a 10 mile *block*, the factor, by which the number of organisms seen in a single microscope traverse should be raised, is 40. Therefore the correct factor in each case can be determined by dividing 200 by the ratio listed. Without going into detail one can make the generalization that whereas 40 is a reasonable estimate of the average ratio in North Sea routes, 30 would be a better figure for the routes "X," "W," and "T." If the results are charted using symbols to represent categories, it is impossible to make any useful correction for these varying factors unless one causes confusion by introducing a whole series of scales for different ratios or for the records to which they apply. For example, if the factor should have been 30 instead of 40, one knows that a number of the observations which were alleged to fall between 440 and 1000 would really have been placed in the next lowest category, 160-440, but clearly there is no means of deciding which particular observations. So some caution will be necessary in interpreting those charts which are used in subsequent 'Bulletins,' at least until the ratios are standardized in the future. It should be stressed, however, that these variations in the factors have no effect on those larger organisms which are actually counted with the naked eye, or on the results for 1946 and 1947 (when it was possible to adjust the factor for the ratio because actual counts were made). Nor need they influence the validity of comparisons of population density which are based on the average values of numbers of samples, because the *accepted value* for each sample included can be corrected before the average is calculated.

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# EXPLANATION OF PLATES IX TO XVI.

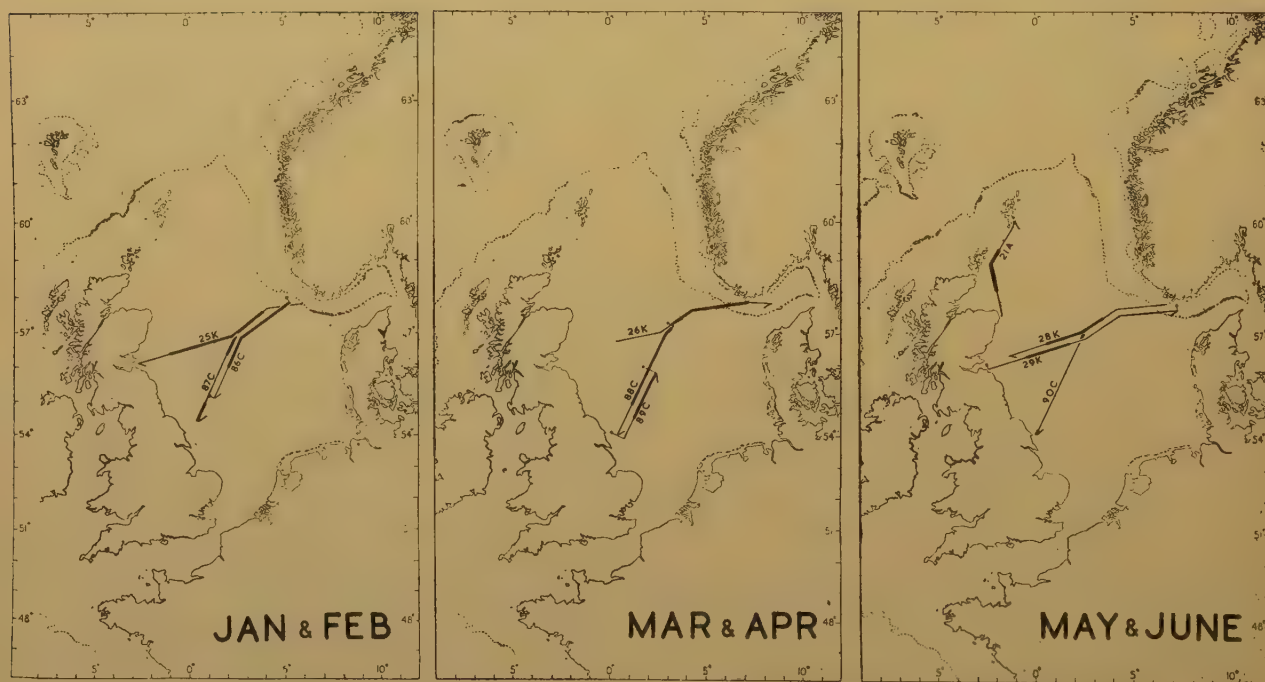
Monthly charts of the Recorder tows taken between January, 1946, and December, 1949. The position and extent of each record is shown by a line against which is placed its serial number and route letter and the date or dates on which it was taken can be found by reference to Table I (p. 141). The half arrow-head at one end of the line indicates the direction in which the tow was made and those parts of a record taken between sunset and sunrise are shown by a thicker line than those taken during the daytime.

The broken lines represent those records or parts of records which were considered to be of qualitative rather than quantitative value because of some slight mechanical defect.

Here and there, when more than one tow was taken over the same route in a month, it has been necessary to displace a record on the chart; then arrows at each end of the line indicate its correct position. When a number of extra tows were taken, those not illustrated are listed on the chart in a marginal note.

## PLATE IX.

## HULL BULLETINS OF MARINE ECOLOGY, Vol. III. No. 21.

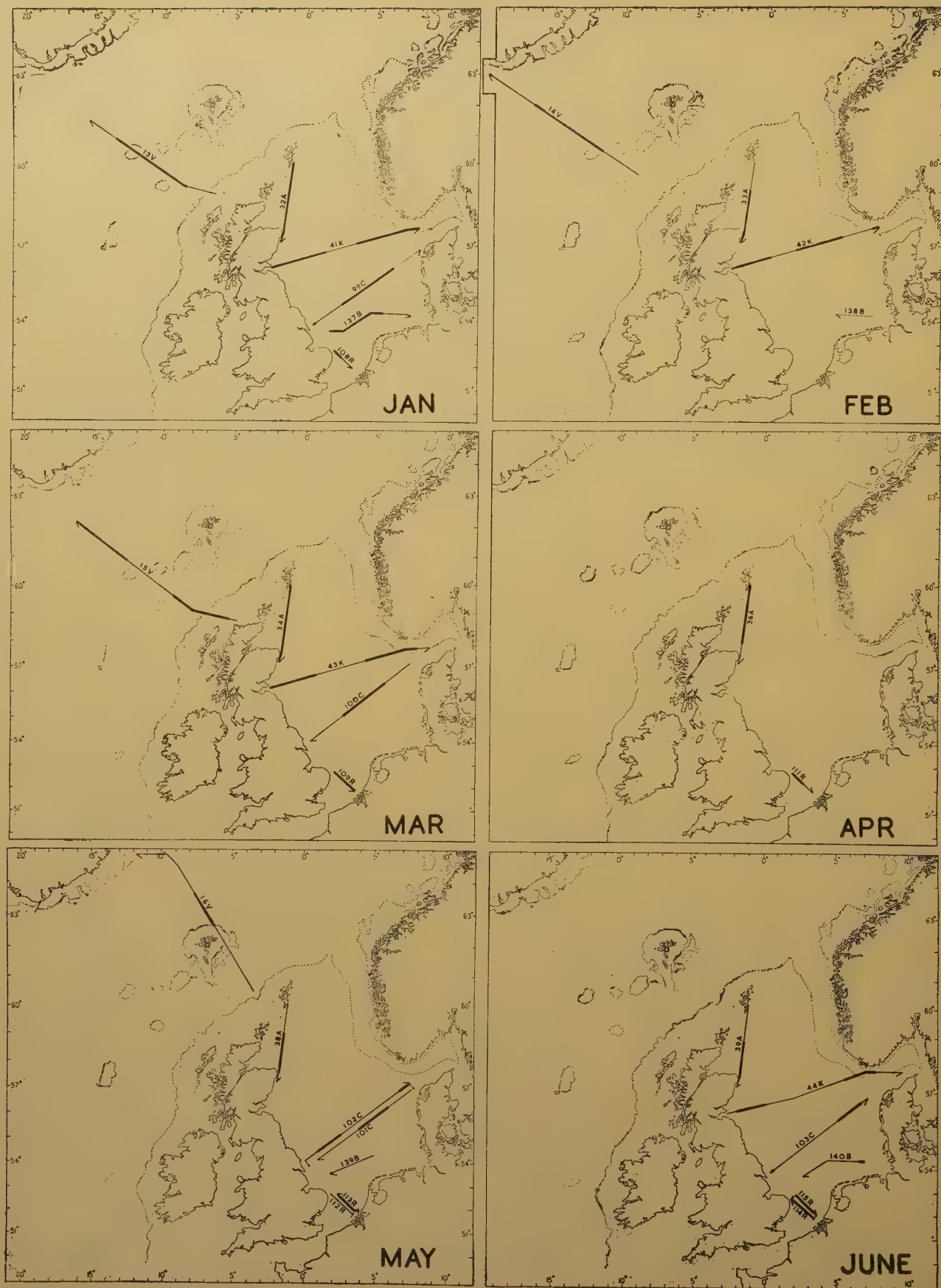


Plankton Recorder lines, January to June, 1946 (see explanation above).

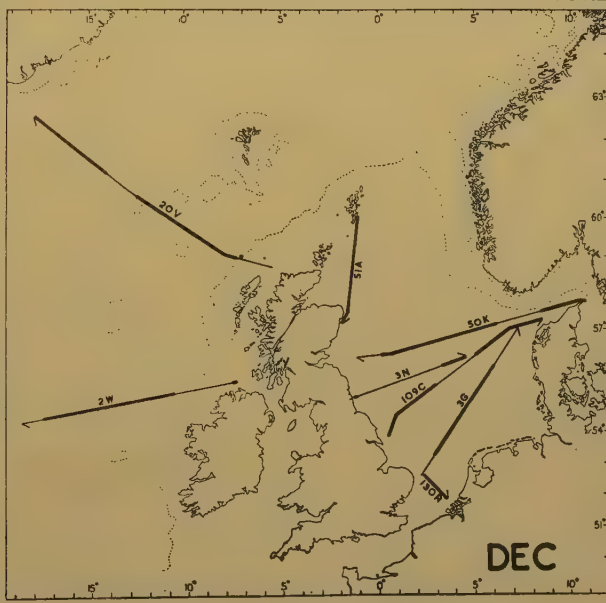
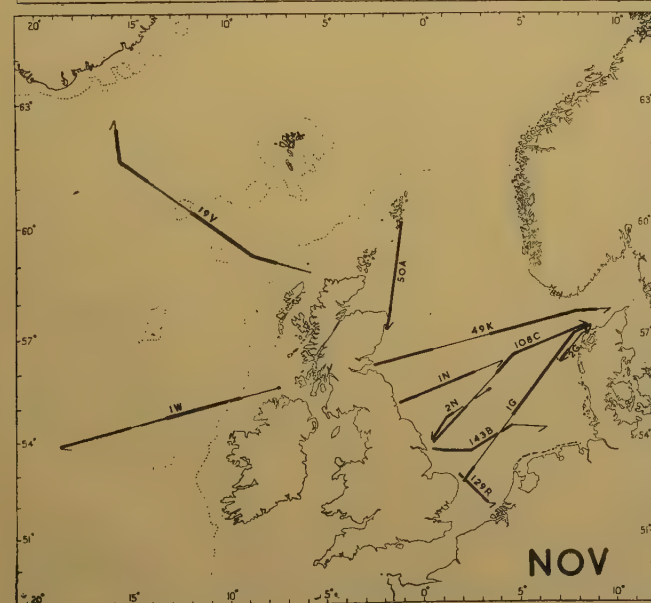
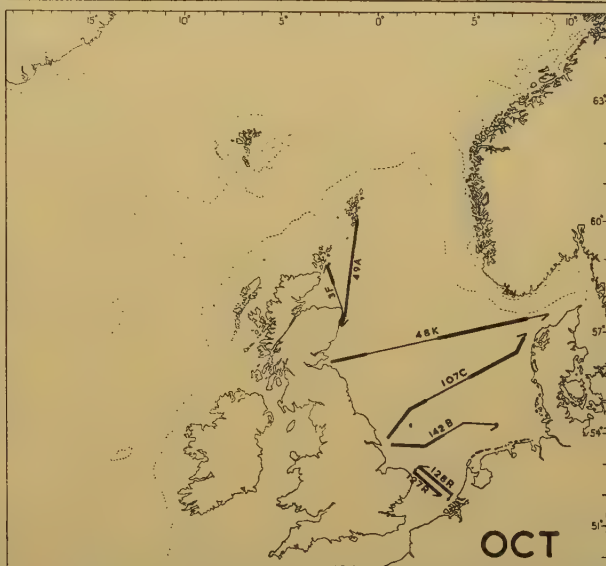


Plankton Recorder lines, July to December, 1946 (see explanation on Plate IX.).

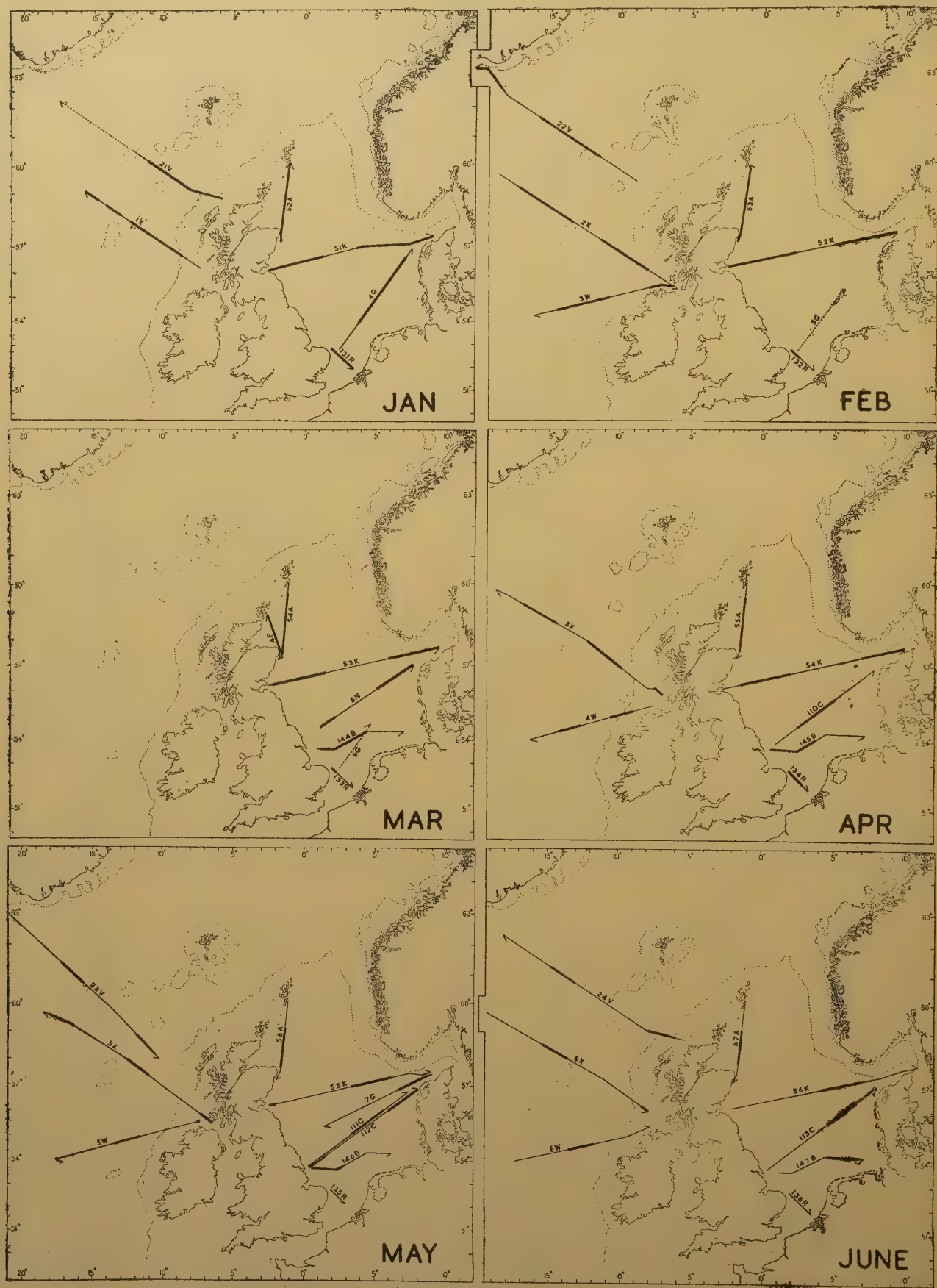




Plankton Recorder lines, January to June, 1947 (see explanation on Plate IX).

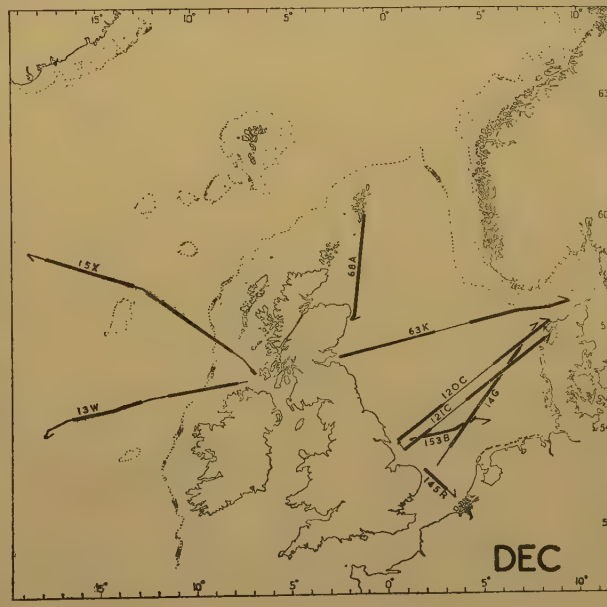
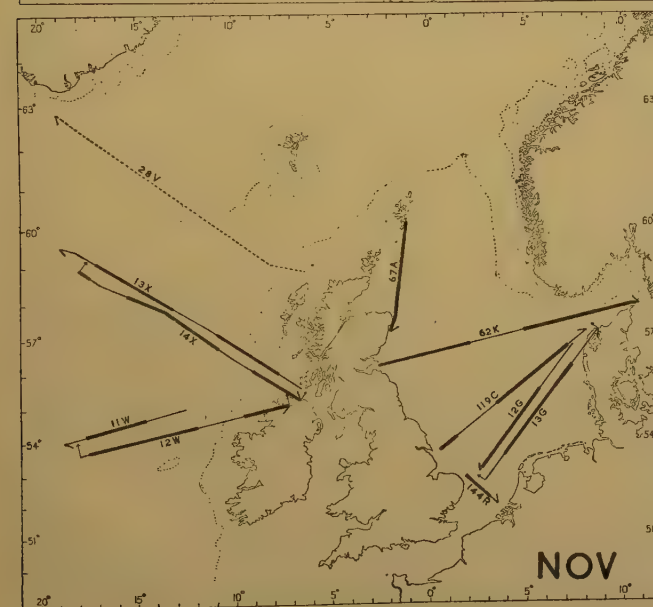
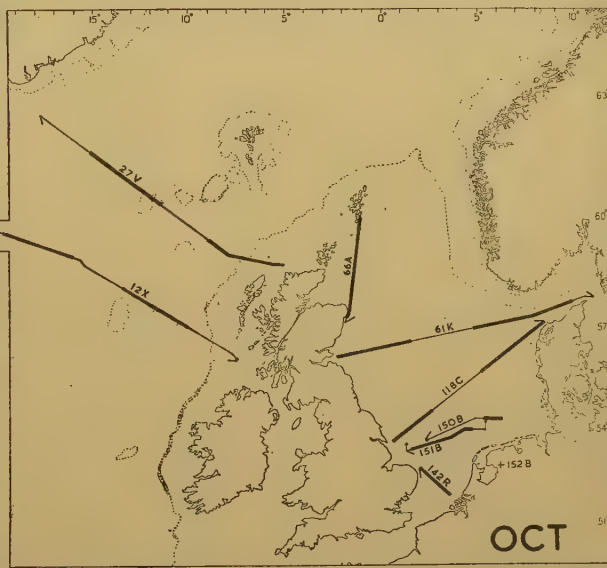
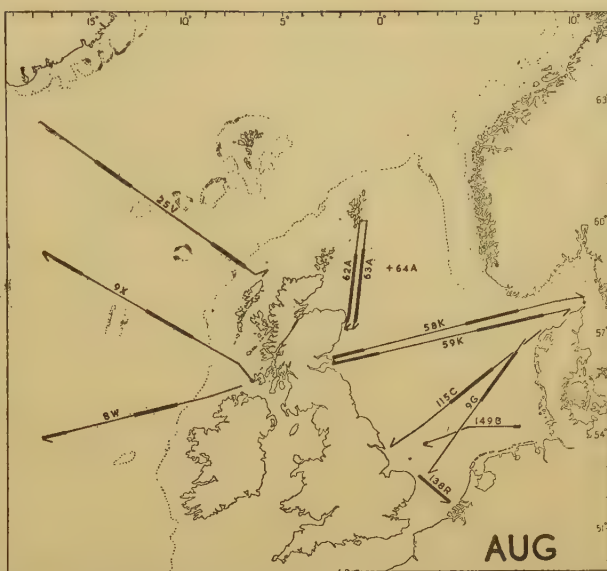


Plankton Recorder lines, July to December, 1947 (see explanation on Plate IX).

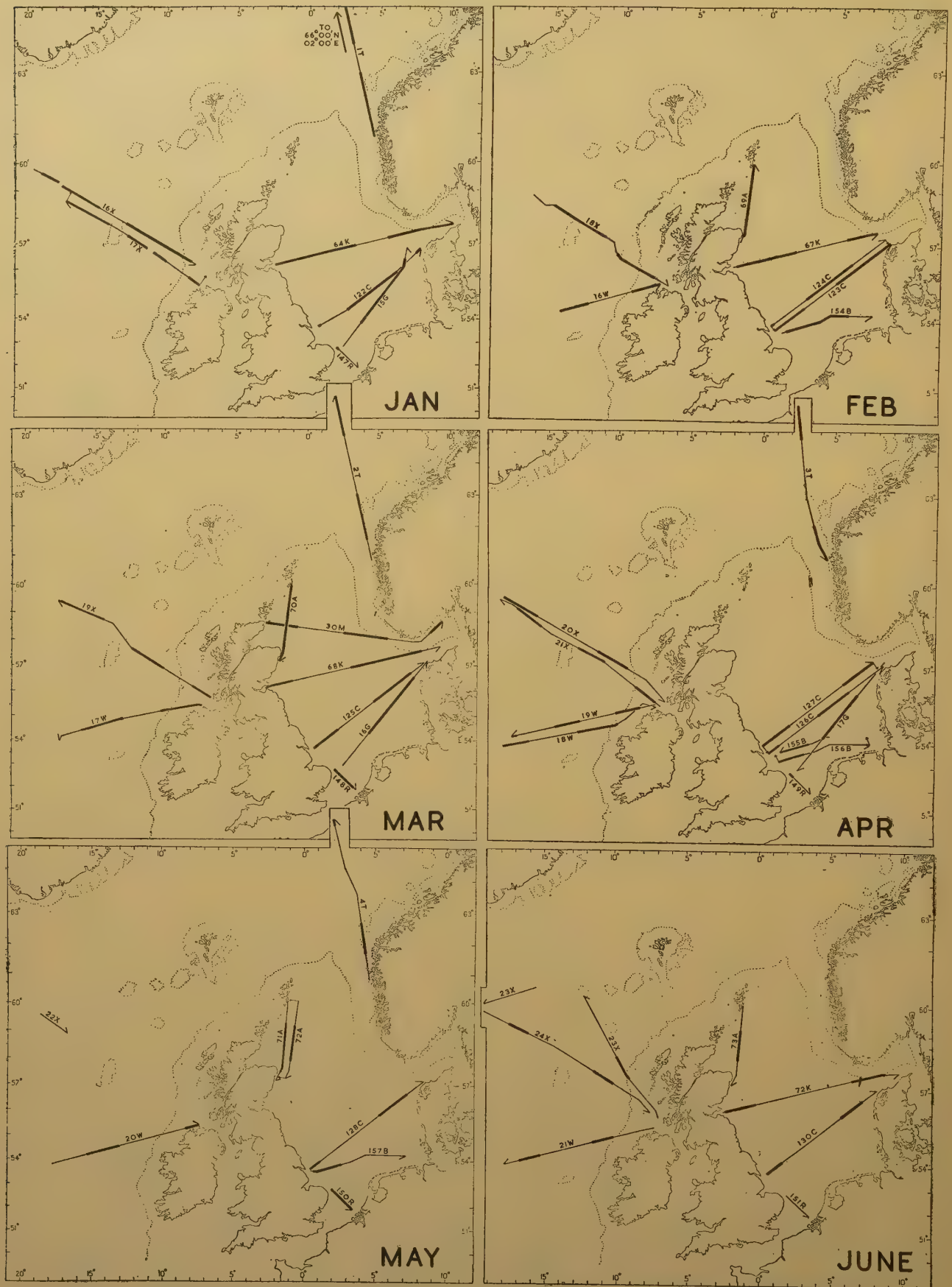


Plankton Recorder lines, January to June, 1948 (see explanation on Plate IX).

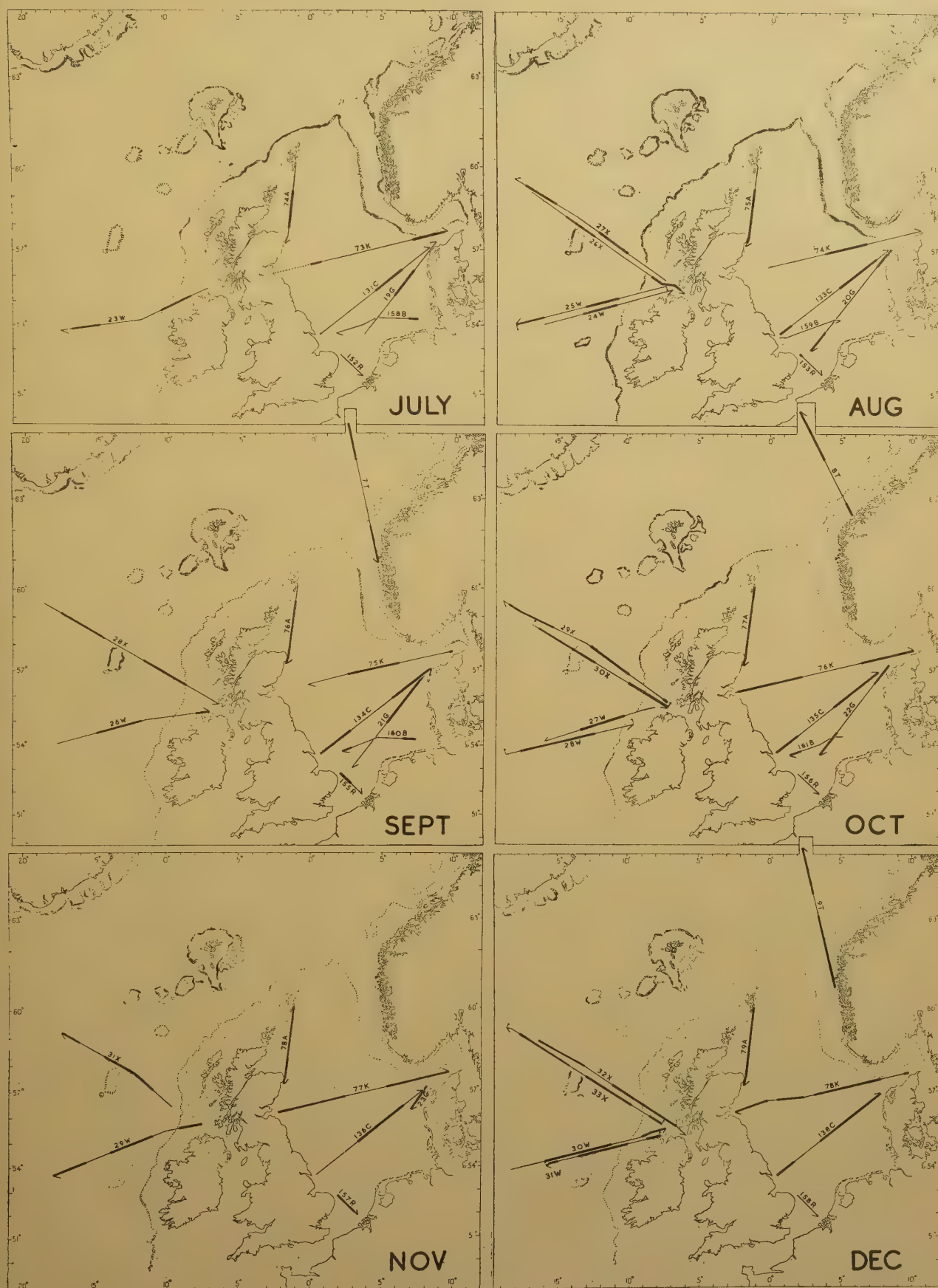




Plankton Recorder lines, July to December, 1948 (see explanation on Plate IX).



Plankton Recorder lines, January to June, 1949 (see explanation on Plate IX).



Plankton Recorder lines, July to December, 1949 (see explanation on Plate IX).





# CONTINUOUS PLANKTON RECORDS: THE DECAPOD LARVAE IN THE NORTH SEA, 1947-1949.

BY

C. B. REES, D.Sc.

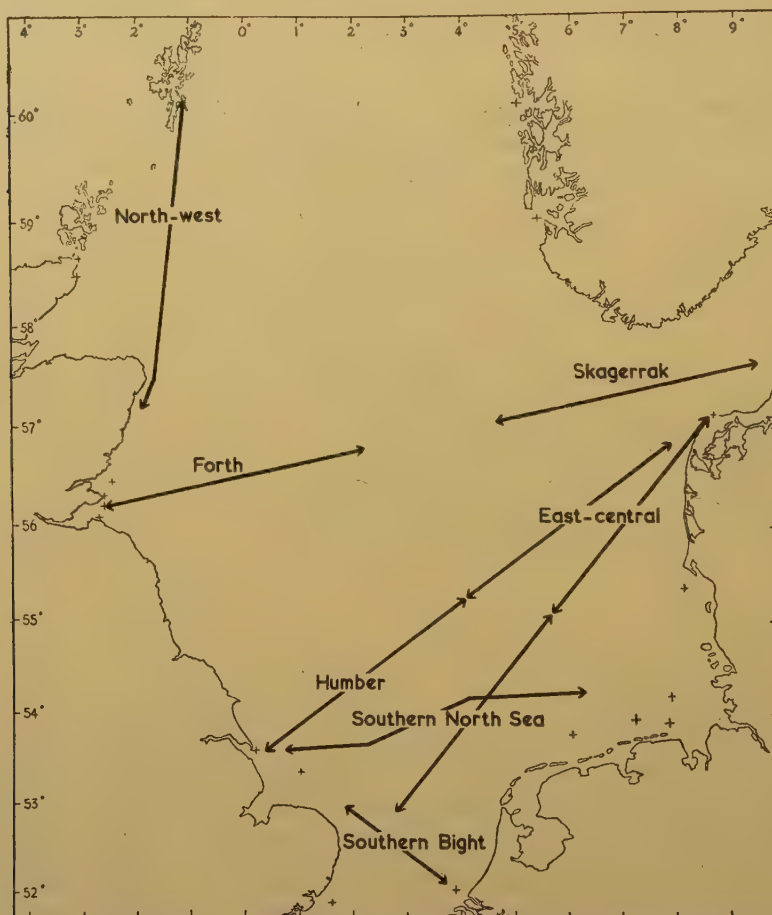
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## INTRODUCTION AND ARRANGEMENT OF DATA.

When the Recorder Survey of the North Sea was resumed after the war it was decided to study the distribution of the pelagic larvae of bottom-living animals, the widespread coverage and regularity of sampling being very advantageous for this purpose. Benthic animals are of great importance as food of demersal fish, and it was thought that a study of their larvae could make a substantial contribution towards our understanding of the economy of the sea. It is well known that many benthic animals fluctuate greatly in numbers and in location, and it is, perhaps, through the larvae that the most immediate explanation of these fluctuations may be found, or should be sought. A more direct consideration is that the larvae themselves may be valuable as fish food. Savage (1931), for example, found that decapod larvae sometimes formed an important part of herring food, and Lebour (1933) has drawn attention to the economic value of molluscan larvae as food for young fish. The first requirement, however, is a definition of the standard pattern of distribution, so that trends and unusual occurrences can be recognized and assessed.

The larvae of three groups of benthic animals, lamellibranchs, decapods and echinoderms, are numerous in the recorder collections. A preliminary account of the distribution of lamellibranch larvae has already been given (Rees, 1951); it will be some time before any similar report on echinoderm larvae is available. The larvae of the polychaetes, another group of great value as food, are surprisingly scarce in recorder collections.



TEXT-FIG. 1.—Chart showing the sections of Recorder lines mostly used in this report, together with the regional terms employed.

The standard recorder routes mainly considered in this report are shown in Text-fig. 1; the extent of sampling achieved in each month is given by Rae (1952). The actual mileage sampled is, in fact, most important, and to disregard it may easily lead to false interpretations of the results. Though sampling is continuous, each record is divided into 10-mile units of tow for the purpose of plankton analysis, and plankton counted or estimated per "10-mile sample." The decapod larvae



were counted and identified in all 10-mile samples taken from the North Sea during 1946-48, but only in the samples analysed for general plankton during 1949. In effect, therefore, the detail was reduced in 1949 because, as Rae (1952) has explained, only half the 10-mile samples, every alternate one, were analysed for general plankton; every sample, however, of the Hull-Rotterdam line was analysed.

Larvae were referred mostly to species, in a few cases to genus only (*e.g.*, *Portunus*, *Hyas*); less than 1% of all larvae examined were unidentifiable. The results for 1946 are, in the main, not included, since the collections in this year were too irregular to give results that may suitably be compared with those of 1947 to 1949.

The distribution of the species and genera are shown in two types of charts (Plates XVII-XIX). One type, used for the uncommon forms, shows every occurrence (usually as +) during the period. In order to review the larval seasons of the uncommon species the number of larvae obtained in each month (1947-49 combined), over the entire North Sea, is shown in Text-fig. 8.

The other type of chart, used for the more common species, shows also the density; the highest number taken over 20 miles of tow throughout one year is represented by a symbol, in accordance with the scale given on Plate XVII. The unit of 20 miles has been chosen so that the charts for 1949, when only alternate samples were analysed may be directly comparable with those for 1947-48. Although compressed as they must be, such charts are useful in showing the overall distribution of a species, they give, in fact, only selected observations, the highest numbers. These common species, however, are further illustrated by means of graphs (Text-figs. 5, 6 and 7) which show the average number of larvae per 10-mile sample per record or fixed section of record. When a particular record was unsuitably short or when it deviated too greatly from the standard route, and thus sampled a different area, the average has not been determined. In a few cases no averages are shown for a whole year, since there may be little advantage in presenting a few values when the suitable records for the year are insufficient to show adequately the seasonal trend in numbers.

Regarding the graphs it is, perhaps, unnecessary to mention that a peak number in the graph does not necessarily indicate that there was on that date a maximum number of larvae in the sea. The best that can be said is that a maximum of unknown amount, but above a certain relative value, probably occurred in the sea some time between the dates of the two records on either side of that which collected the highest number of larvae. Clearly, too, it may only be said that larvae first appeared in the plankton (above the threshold of density required for collection by the recorder) some time during the interval between two records, that on which larvae were first collected and the previous one. As a general rule there is no significance in the difference between highest numbers in collections; to compare numbers obtained in different years or regions attention must be directed not to single densities, but to the level of density maintained over, say, three successive observations in each year or region.

The regional terms used throughout this report are determined by the most suitable way of using and dividing recorder lines (Text-fig. 1), and may differ somewhat from those commonly used. The "north-west" was covered by the whole of the Aberdeen-Lerwick line. The Leith-Copenhagen line has been split, the first 160 miles covering the "Forth" region and the section 240-400 miles the "Skagerrak" region. The Hull-Copenhagen line has also been split into a western half, the "Humber" region and an eastern half, the "east central" region. The "southern North Sea" was covered by the Hull-Bremen line and the "Southern Bight" by the Hull-Rotterdam line. The London-Copenhagen line passed over two regions, the southern North Sea and east-central regions. Unfortunately, the Heligoland Bight was rarely sampled throughout 1946-49. So few larvae were found on the central part of the Leith-Copenhagen line that it is not worth while dealing with their distribution.

#### THE INFLUENCE OF VERTICAL DISTRIBUTION.

All the present results are derived from horizontal hauls at a depth of 10 m., and much thought has been given to the question of how they may be influenced by the vertical distribution of decapod larvae as shown by Russell (1927*a*, 1931), Jorgensen (1923) and Savage (1926).

Regarding the changes in vertical distribution of a single species due to seasonal, diurnal, hydrographical and weather conditions (Russell, 1927*a* and *b*), reference to the results themselves provides a satisfactory answer. To do this in detail at this point, however, would necessitate too much reference forward. It can be said with confidence that the results are regular, consistent, and in agreement with those of other workers to a degree which renders it most unlikely that the trends found are determined or affected by changes in vertical distribution. It is worth emphasizing that we have little concern with the number occurring on a particular 10-mile sample. Our concern is with the trend shown by a *series* of observations in time, each of which consists of an average number of larvae derived from a *series* of 10-mile samples. The series of 10-mile samples are taken during a towing period lasting about 18 hours, with the result that variations in numbers due not only to patchiness in horizontal distribution but also to changing vertical distribution, especially those due to diurnal migration, are smoothed out.

Russell (1927*b*) shows that various species, and stages of the same species, occupy different depth zones. The relative numbers of a group of species collected at 10 m. would not, therefore, be the same as the relative numbers taken in vertical hauls. Nevertheless, the present results are comparable *inter se*.

It must be conceded that regional differences in the vertical distribution of a particular species (Russell, 1927*b*) present a difficulty. These regional differences may be inconsiderable, within the confines of the North Sea, but some care is required if one desires to compare the numbers of larvae of a species caught in one region with the numbers caught in a widely separated region.



It should be noted that the magnitude of the changes in number found was considerable. Ten examples have been taken at random from Text-figs 5-7; the average increase of the maximum number of larvae over the number on the record previous to that with the maximum was calculated as approximately eleven-fold. In contrast, Savage (1926) found an increase of only 11% in total decapod larvae in his mid-water hauls at night, less in his surface hauls. As a further contrasting example we may take the results of Russell (1925), and compare the average percentage of larvae in his 1st and 5th series (day) with the average in his 2nd (dusk), 3rd (dark) and 4th (dawn) series at the depth of 9-16 m. Giving the day average first, the values for Galatheid larvae are 17.6%, 21.8%; *Porcellana* 40.5%, 28.0%; *Callinassa subterranea* 34.8%, 21.9%; *Upogebia* 33.8%, 25.1%; Pagurid larvae 10.6%, 19.3%; crab zoeae 30.5%, 26.8%. In no case is one figure twice as big as the other.

Another general consideration is that the depth of 10 m. may be a singularly favourable one. The changes in vertical distribution are not shown equally at all levels, and it may be that relatively minor changes occur at a depth of 10 m. In this connection it is of particular interest to compare the analysis by Rae and Fraser (1941) of Savage's data for *Pseudocalanus* and *Temora*.

It appears unlikely, therefore, that the results obtained are affected to any important extent by vertical distribution and its changes. As in many other cases arising from recorder material, the differences we are interested in appear to be much greater than differences that may arise through changing vertical distribution.

#### THE DISTRIBUTION OF TOTAL DECAPOD LARVAE.

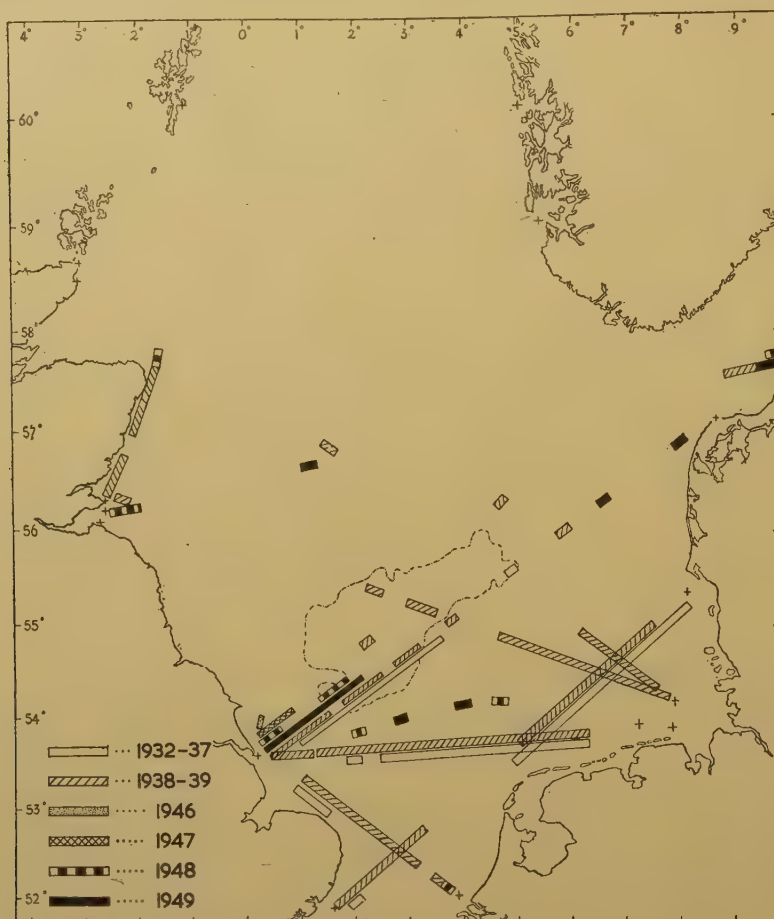
Before the war the species of larvae were not determined and counts and estimates were made of total decapod larvae only. The distributions for the period 1932-37 are given by Henderson and Marshall (1944), and for the period 1938-39 by Marshall (1948). These earlier distributions, together with those for each year 1946 to 1949, are given in summarized form in Text-fig. 2, the distribution of all 10-mile samples with more than 50 decapod larvae being shown. In Text-fig. 3 the distribution of all 10-mile samples with more than 100 larvae is shown. It is intended that these two figures should be compared with those for lamellibranch larvae (Rees, 1951, Text-figs. 1 and 2).

There is a marked difference between the main concentrations of lamellibranch larvae and of the decapod larvae. Whilst the former were chiefly east and northwards of the Dogger Bank, the latter were chiefly south, from the Humber into the Heligoland Bight. The distribution of lamellibranch larvae can largely be related to swirls (Rees, 1951), but such an explanation seems unsatisfactory in the case of decapod larvae. Both groups had their highest numbers about the same time, July and August, so that the difference in distribution cannot have arisen through a seasonal change in the system of currents and swirls.

The generalized water circulation of the North Sea, as shown by Böhnecke



(1922), suggests that the Dogger Bank may be regarded as a partial barrier between water to the north and water to the south. Though the Jutland current breaks out northwards, the Heligoland Bight swirl also tends to retain water in the south. This being so there is a tendency to limit the southern pelagic forms from extending



TEXT-FIG. 2.—Chart showing the distribution of 10-mile samples with more than 50 decapod larvae, during the periods 1932-37, 1938-39, and each year from 1946 to 1949.

northwards. It may be thought, therefore, that the distribution of decapod larvae correctly shows that adult decapods are most numerous in the shallower water of the southern North Sea.

The average number per 10-mile sample per record or section of record is shown in Text-fig. 4. In all regions a major peak in numbers occurred in July or August. It is interesting to note that Savage (1931) found that the number of decapod larvae in herring stomachs reached a very definite maximum in August. When sampling was adequate there was, with a high degree of consistency, a very

small peak in April or May. This reflects the fact, as will be observed later, that species tend to fall into either of two main hatching periods, April-May or August.

It is noticeable that 1947 was a poor year for decapod larvae in most regions. It may be observed, however, that some recorder lines deviated considerably from



TEXT-FIG. 3.—The black rectangles show the distribution of all 10-mile samples, obtained during the entire Recorder Survey, with more than 100 decapod larvae.

the standard routes during the year, and this fact may partly explain the extremely low numbers obtained in the Skagerrak and east-central regions, but not the comparative scarcity off the Forth and Humber.

#### DISTRIBUTION OF THE SPECIES OF DECAPOD LARVAE.

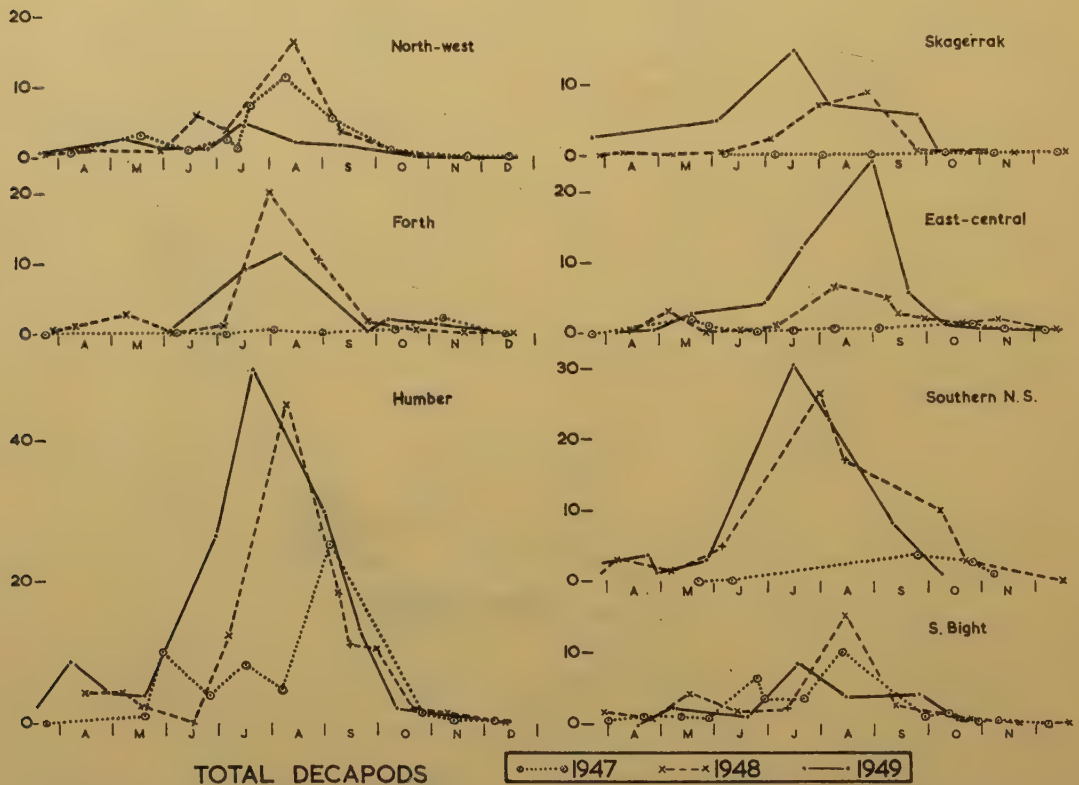
The nomenclature of Balss (1926) is used.

*Pandalus montagui* Leach.—(Plate XVII.) The larvae were uncommon, only 67 being recorded during the three years. Though of fairly scattered occurrence, most of the larvae came from the Forth and Humber regions.

(Text-fig. 8.) A distinct peak in numbers occurred in April, with a secondary peak in August.

Thorson (1946) gives the larval season as mid-May to October. Jorgensen (1923), whose samples began in mid-May, found the largest number in July and August, and Lebour (1947) says that larvae occur in spring and summer, with a few in autumn.

*Pandalina brevirostris* (Rathke).—(Plate XVII.) Only 73 specimens were recorded. They were distributed rather like those of *Pandalus*, but there were proportionately more in the north-west. Thus, 45% of all specimens of *Pandalus* occurred on the Aberdeen-Lerwick and Leith-Copenhagen lines, whereas 70% of all specimens of *Pandalina* were found on these lines.



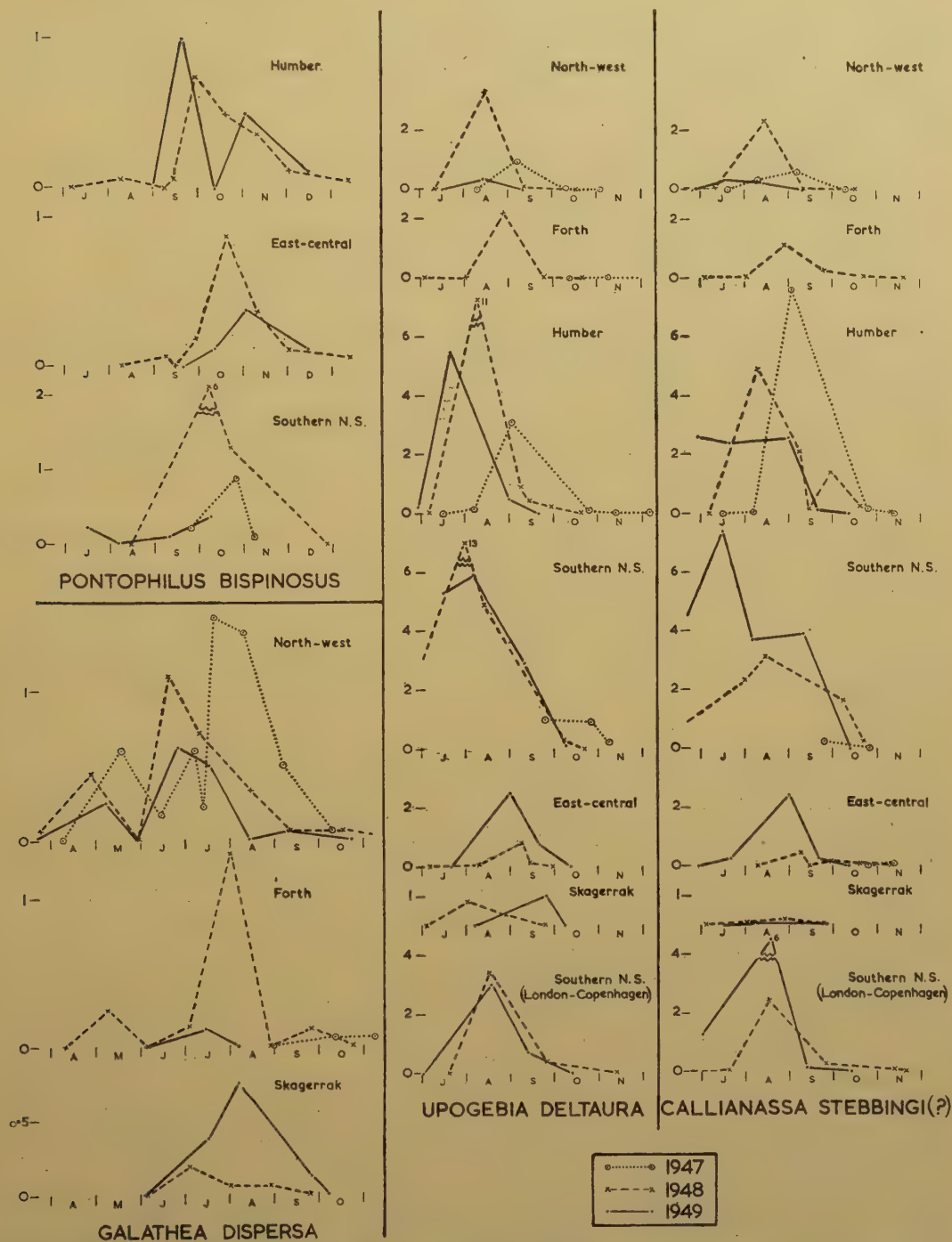
TEXT-FIG. 4.—Graphs showing the number of decapod larvae, all species combined, per 10-mile sample of each record in the regions shown in Text-fig. 1.

(Text-fig. 8.) The peak number occurred in August. A secondary peak is shown in May, but this probably has no significance. Lebour (1947) records larvae as very common in spring and summer. Thorson (1946) gives the larval season as mid-July to late September, and Jorgensen (1923) found that hatching took place throughout the summer.

*Hippolyte varians* Leach.—(Plate XVII.) Larvae were uncommon, only 45 specimens being observed throughout 1947-49. Most of these were found off the Humber and in the Southern Bight.

(Text-fig. 8.) The maximum number occurred in October, and a few specimens were found even as late in the winter as January. Lebour (1947) obtained larvae throughout the year, the largest numbers in September and October.





TEXT-FIG. 5.—Graphs showing the number of larvae of some decapod species per 10-mile sample of each record in various regions. The regions are shown in Text-fig. 1,

*Caridion gordonii* Bate.—(Plate XVII.) Only 14 larvae were observed throughout 1947–1949. Eleven of these were obtained in July and August, 1947, and one in August, 1948, on the Aberdeen-Lerwick line. Of the remaining two larvae one was found in June, 1948, and the other in July, 1948, over the Great Fisher Bank. The June specimen was in Stage I, suggesting that it did not appear there as a result of transportation from any considerable distance to the north or north-west.

*Processa canaliculata* Leach.—Two badly damaged larvae may possibly be of this species, but it is not certain. One was obtained off the Aberdeenshire coast in April, 1947, and the other, a very late stage, off the Forth in September, 1948.

*Processa edulis* Risso.—(Plate XVII.) The larvae were rare, only 11 specimens being obtained in 3 years. They were observed from July to October, mostly in August.

*Processa aequimana* Paulson.—(Plate XVII.) The presence of these larvae in the North Sea has already been reported (Rees and Cattley, 1949). No specimens were obtained in 1946, 7 in 1947, 29 in 1948 and 14 in 1949. For comparative purposes the number obtained in 1949 must be doubled, since only half the 10-mile samples were analysed. (This point should also be remembered when comparing the charts for each year.) There appears, therefore, to be little difference between 1948 and 1949, and the view expressed by Rees and Cattley that numbers may be increasing from year to year is not confirmed for 1949. However, the estimate of 28 for the year is such a small number that it may not be taken as being definitely in disagreement.

Larvae were obtained from June to November, the greatest number being obtained in August.

*Crangon crangon* (L.) and *C. allmanni* Kin.—(Plate XVII.) The total number of specimens obtained of each species was very similar, about 150, but *C. allmanni* was found on 99 occasions and *C. crangon* only on 65. *C. crangon* was found almost entirely in the south, over 60% of all specimens occurring on the Hull-Rotterdam line. *C. allmanni*, though mainly concentrated in the south (35% of all specimens were found on the Bremen line), occurred more frequently than *C. crangon* in the north. The difference is shown by the fact that only 4% of all specimens of *C. crangon* were found on the three most northerly lines as against 33% of *C. allmanni*.

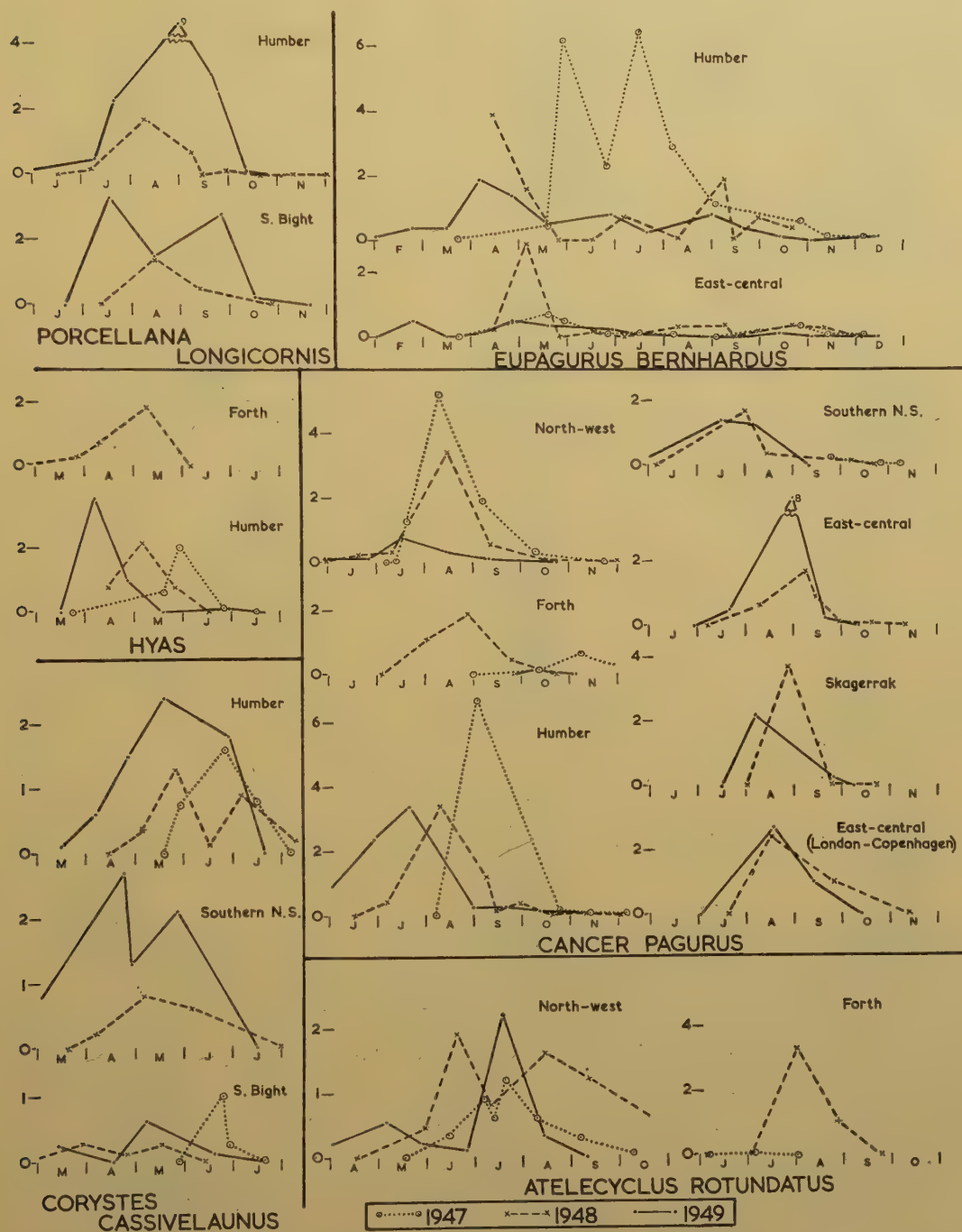
(Text-fig. 8.) A relatively great number of *C. crangon* were found off the Dutch coast in January, 1948, thus accounting for the large peak in this month. These larvae presumably had hatched from eggs spawned the previous October or November. Lebour (1947) states that larvae of *C. crangon* occur practically throughout the year, and may be numerous in any month from April to August. Thorson (1946) found larvae of *C. crangon* from mid-May to early October, and of *C. allmanni* from mid-April to late July. Lloyd and Yonge (1947, p. 645) summarize earlier results on spawning seasons of *C. crangon* in the North Sea.

Although numbers were low, there seems little doubt that 1948 was the best year for both species and 1949 the poorest year for *C. crangon*.

*Pontophilus bispinosus* Hailstone and Westwood.—(Plate XVII.) Though of widespread occurrence, the larvae were found mainly south of the Dogger Bank but not in the Southern Bight. Unlike many other species, the number off the Humber was not relatively high. The main concentration was found in 1948.

(Text-fig. 5.) The peak numbers occurred rather late in the year, in September–October. The difference between 1948 and 1949 is not marked off the Humber; no larvae were found in 1947. Lebour (1947) obtained larvae from March to October, and Thorson (1946) found them chiefly in September.

*Pontophilus trispinosus* Hailstone.—(Plate XVII.) Larvae were uncommon, only 55 specimens being observed throughout 1947–49. It should be remembered that only half the samples were analysed in 1949 as against all in 1947 and 1948. The distribution is of interest in the grouping of observations, indicating a stability in distribution. The Southern Bight observations of 1947 and those of the southern Dogger in 1948 occurred in each month from



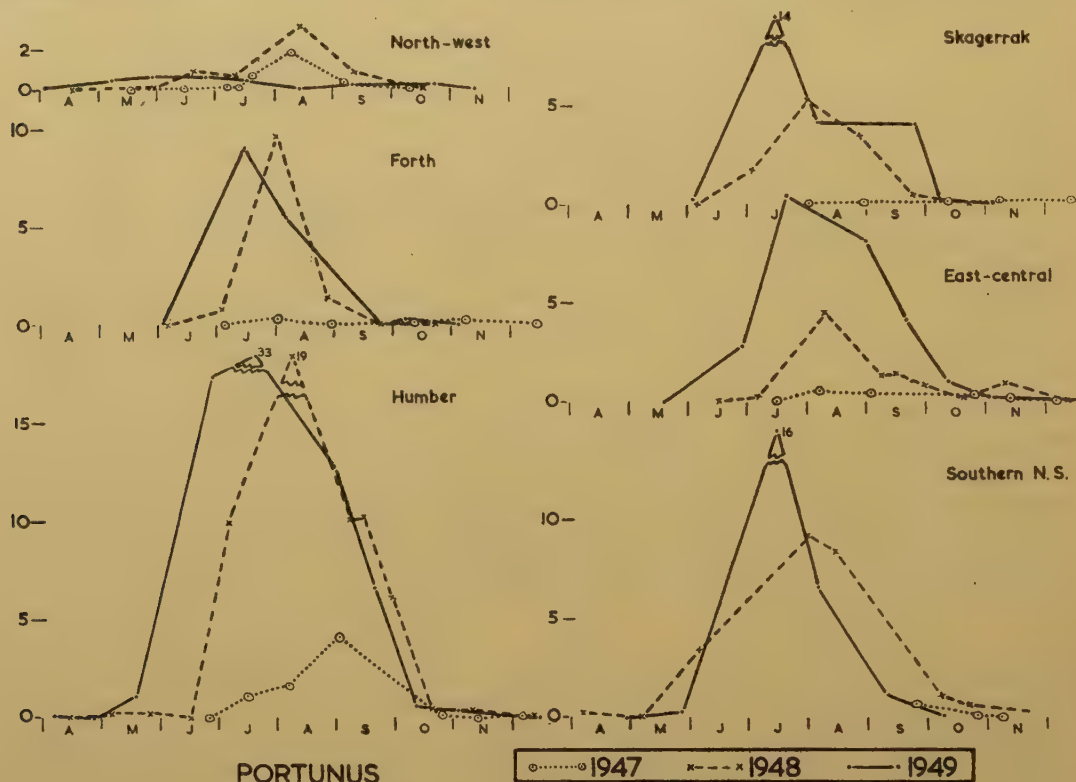
TEXT-FIG. 6.—As for Text-fig. 5.



August to November, *i.e.*, larvae of *Pontophilus trispinosus* were found within restricted areas over several months.

(Text-fig. 8.) Most larvae were found in September. Lebour (1947) says that the larvae occur in spring and summer. 1948 was the best year for the larvae, and they appeared earlier in the collections in this year than in 1947 and 1949.

*Pontophilus spinosus* (Leach).—A single specimen was obtained in May, 1948, off the Aberdeenshire coast.



TEXT-FIG. 7.—As for Text-fig. 5, but of *Portunus* only.

*Nephrops norvegicus* (L.).—(Plate XIX.) One specimen was obtained to the east of the Dogger Bank in December, 1947, and three specimens near the Forth in August, 1948.

*Upogebia stellata* (Montagu).—(Plate XIX.) *U. deltaura* and *U. stellata* have so rarely been distinguished in the adult that Balss (1926) found it necessary to define their joint distribution in the North Sea. For a long time the larvae of *Upogebia*, collected by the recorder, were separated into species, but it appeared that the larvae of *U. stellata* were very rare in comparison with *U. deltaura*, and little error would result if all *Upogebia* larvae were considered to be *U. deltaura*. The separation of the species of larvae is not easy.

What few observations are available of *U. stellata* are given in Plate XIX. Larvae were observed in September, 1946, October and November, 1947, and July and August, 1948. Thus larvae appear at the same season as those of *U. deltaura*.

*Upogebia deltaura* (Leach).—(Plate XVII.) The larva was common, and concentrations were found in several places, off the Scottish coast, Humber, Skagerrak, Danish coast and southern North Sea, but rarely in the Southern Bight,



TEXT-FIG. 8.—Histograms showing, in each month, 1947-49 combined, the total number of larvae of some species obtained over the entire North Sea.

(Text-fig. 5.) The general tendency is for the peak in numbers to be sharply defined; this makes it the more difficult to compare years, since the date of collection on a particular line must have been of great importance. Nevertheless, the curves for the three western areas (north-west, Forth and Humber) are consistent in that the highest number occurred in 1948 and that the peak number was obtained earlier in 1948 than in 1947. This latter feature is shown beyond doubt only off the Forth. (In 1949 no suitable results are available here due to short records in August and September.)

During identification, early stages (Stages I and II) were separated from late stages (Stages III and IV), and the separate results in two areas in 1949 shown in Text-fig. 9. The graphs confirm that only one main breeding occurred, as, of course, is indicated in Text-fig. 5.

Lebour (1947) found larvae commonest in July to September, but present from April to November.

*Callianassa stebbingi* Borradaile (?).—Larvae of two species of *Callianassa* occur in the North Sea. I am unable to distinguish one of these from that of *C. subterranea* as described by Webb (1921) and Gurney (1942) and the other from that of *C. stebbingi* (= *laticauda*) as described by Gurney (1942). The first larva is abundant and widespread in the North Sea; the other is rare and found only on the Hull-Rotterdam line, i.e., it may well be an immigrant from the Channel.

Turning now to the adults, Balss (1926) states that the North Sea species of *Callianassa* is *C. stebbingi*, and that *C. subterranea* is a pure south of England species. Selbie (1914) states that it is doubtful whether the real *C. subterranea* has been taken anywhere except on the south coast of England.

The situation is, therefore, that the distribution of the larva *C. subterranea* agrees very well with the distribution of the adult *C. stebbingi*, and does not agree at all with that of the adult *C. subterranea*: conversely for the larva *C. stebbingi*. Since it is proposed, later, to relate the distributions of larvae and adults, the larva which appears to be identical with that described by Gurney (1942) as *C. subterranea* will be referred to in this report as *C. stebbingi* (?) and the other larva as *C. subterranea* (?).<sup>1</sup>

(Plate XVII.). The larva had a widespread distribution, and closely resembled that of *Upogebia deltaura*.

(Text-fig. 5.) There is a close correspondence between these graphs and the corresponding ones for *Upogebia deltaura*. Graphs for the two species in the north-west are very similar, with *Callianassa*, however, first appearing in the records a little earlier than *Upogebia* in each year. In the Forth region, too, the species were similar except that no *Callianassa* were found in 1947. It appears that off the Humber the numbers stayed relatively high for 2 months or so. High numbers appeared successively earlier from 1947 to 1949. In the southern North Sea larvae were more numerous in 1949 than in 1948, and probably appeared somewhat earlier. In the east-central region, too, larvae appeared earlier in 1949 than in 1948.

Young stages and late stages are shown separately in Text-fig. 9, as for *Upogebia*. There did not appear to be such a decrease in numbers, at 10 m. depth, between young stages and late stages as in *Upogebia*. A reading of the graphs suggests that the period of development of *Callianassa* was longer than in *Upogebia*.

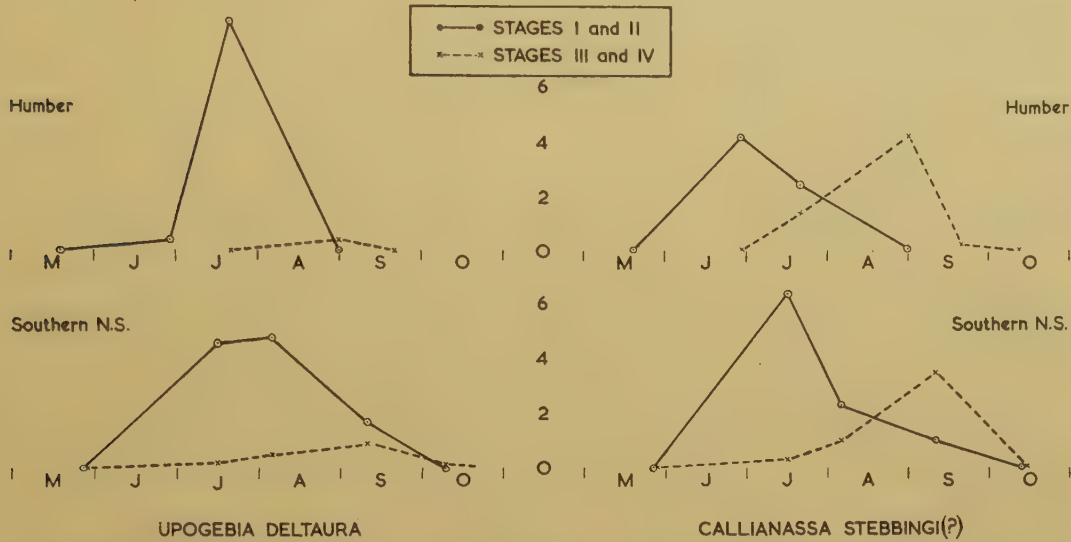
*Callianassa subterranea* Mont. (?).—(Plate XIX.) As explained under *C. stebbingi* (?), this larva seems to be that accepted by Gurney (1942) as belonging to *C. stebbingi*.

All the specimens were obtained in the Southern Bight, 11 in August and 2 in September, 1947; 5 in August, 1948; none in 1949. This larva resembles very closely that of *Thia polita* in distribution, seasonal occurrence and decrease in numbers through the years 1947–1949 (cf. p. 175).

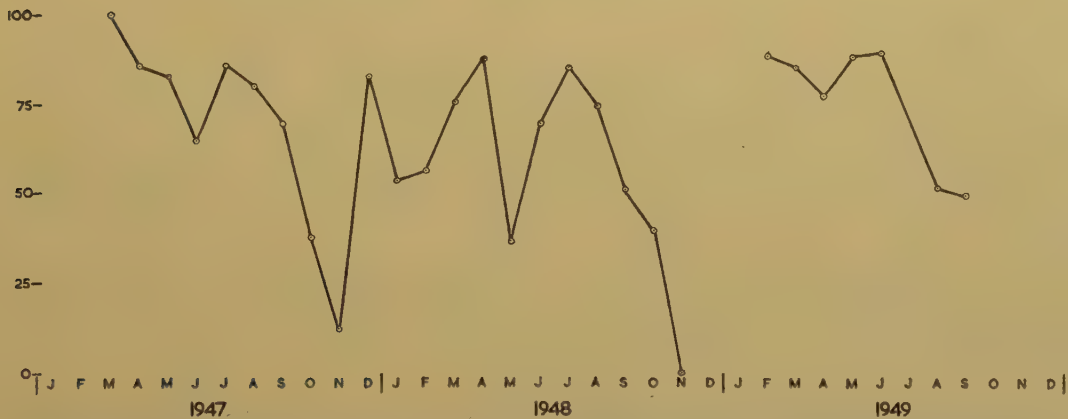
<sup>1</sup> With great diffidence a possible explanation of the discrepancy may be suggested. If *C. stebbingi* and *C. laticauda* are not identical species, then the larvae of *C. stebbingi* and *C. subterranea* may be very similar and the uncommon Southern Bight larva may be that of *C. laticauda*.



*Galathea dispersa* Bate.—(Plate XVIII.) About 250 specimens were observed, as compared with 230 of *G. intermedia*, 66 of *G. squamifera* and 4 of *G. strigosa*. They were chiefly found in the north-west and, in lower numbers, off the Skagerrak. Apart from a very few occasions they were not found off the Humber.



TEXT-FIG. 9.—Graphs, abstracted from Text-fig. 5, but showing separately the young stages (Stages I and II) and later stages (Stages III and IV) of *Upogebia deltaura* and *Callianassa stebbingi* (?).



TEXT-FIG. 10.—Graphs showing, in each month, the percentage of young stages (Stages I and II) of *Eupagurus bernhardus* larvae in total *E. bernhardus* larvae over the entire North Sea.

(Text-figs. 5 and 8.) Despite the low numbers, there were two peaks in each year in the numbers for the north-west. If the 1947 curve is displaced forward about a month, the three curves become virtually coincident in trend. The major peak occurred in June–July, and the secondary peak in April–May. Judging from the general levels of the three curves, 1947 was the best year for the larvae and 1949 the poorest. The succession of larvae, too, was later in 1947 than in the two following years.

A bimodal curve is shown, too, for the Forth area in 1948. In 1947 larvae were obtained only late in the year, September and October (cf. *Cancer pagurus* and *Upogebia deltaura*).

The bimodal curves suggest two main hatchings in the course of the year. The absence of bimodality off the Forth in 1947 and 1949 and off the Skagerrak in 1949 is not significant, since no Leith-Copenhagen records were obtained in April and May of the two years.

*Galathea intermedia* Lilljeborg.—(Plate XVIII.) In this species the main concentration occurred off the Humber, not in the north-west as in *G. dispersa*.

(Text-fig. 8.) Most larvae occurred in July and August. The groupings of all results in this way conceal possible double hatchings during the year, the main one in July and August and a very small one in October–November. Thorson (1946) gives the larval season as late July to late October.

Larvae were more numerous in 1948 than in 1947 and 1949 in the north-west. Off the Forth 1948 was better than 1947; there is insufficient information about 1949. Off the Humber both 1948 and 1949 were good years and larvae were more numerous than in 1947.

*Galathea squamifera* Leach.—(Plate XIX.) Larvae were found mostly in the north-west and around the Danish coast. In the north-west larvae were found in greatest numbers in 1947–48 near to the Shetlands on even-numbered 10-mile samples not analysed in 1949.

(Text-fig. 8.) Considering the trend in the histograms the hatching times of *G. dispersa* and *G. squamifera* seem very similar, *G. intermedia* a little later.

Lebour (1947) found larvae from January to October, most numerous in April and May.

*Galathea strigosa* (L.).—(Plate XIX.) The two specimens in the north-west were found in July, 1947, both in Stage I. The Skagerrak specimens were in Stage III and were obtained in August, 1948.

*Munida* Leach.—(Plate XIX.) Whilst the species have not been distinguished it can be presumed that most, if not all, of the larvae were of *M. bamffia* (Pennant), although the specimen at the Skaw may have been *M. tenuimana* Sars. Nearly all the larvae were obtained in the north-west. A single specimen was observed off the Forth in July, 1946, and two in June, 1949.

(Text-fig. 8.) Most larvae were obtained in May. Numbers decreased in each year from 1947 to 1949.

*Porcellana longicornis* (Pennant).—(Plate XVIII.) The larvae were nearly always taken near to the coast, particularly off the Humber. Since the 10-mile sample nearest to the Shetlands was not examined in 1949 low numbers here in 1949 are without significance.

(Text-fig. 6.) Most larvae were obtained around August. Jorgensen (1923) suggests that there were two distinct hatches of larvae, one in spring and one from July onwards. Lebour (1947) says that the larvae occur in every month except December, being commonest during summer.

It is clear that 1949 was easily the best year for the larvae and 1947 the poorest.

*Eupagurus bernhardus* (L.).—(Plate XVIII.) Though of widespread occurrence the larvae were, quite definitely, most common at the Dogger Bank.

(Text-fig. 6.) The curves for the years are erratic and, unfortunately, numbers were too low on the other lines to assist in the interpretation.

It would seem that, in each year, a main hatching of larvae occurred in April or May. Some hatching continued almost throughout the year.

The percentage each month of Stages I and II in total larvae is shown in Text-fig. 10, taking in all North Sea material. Peaks occur in March, July and December, 1947, April and July, 1948, February and June, 1949. These imply two main hatchings, at least, during a year, in winter and summer.

Thorson (1946) gives the larval season as late March to late October. Jackson (1913) says that the breeding period of *E. bernhardus* is very extended, and larvae may be found in the plankton from April to the end of September.

*Eupagurus prideauxii* (Leach).—(Plate XVIII.) Apart from a single specimen off the Skaw

the larvae were found only in the north-west and off the Forth. They were uncommon, only 22 specimens being found during 1947-49. Larvae were found earlier in the north-west than off the Forth; in 1947 larvae were found in July, September and October in the north-west, in November and January (1948) off the Forth; in 1948 in June, August and September in the north-west, in August and December off the Forth; in 1949 none were found in the north-west, in November off the Forth. In addition one may include the 1946 distributions; in July, August and September in the north-west, in October off the Forth. These timings strongly suggest arrival of the larvae off the Forth as a result of translation from the north-west.

In the north-west more larvae were obtained in August than in any other month.

*Eupagurus pubescens* (Krøyer).—(Plate XVIII.) Larvae extended further south than those of *E. prideauxii*, but were hardly more common, only 28 specimens being found during 1947-49. The larvae appeared during the period February to May, all those in February and March being in Stages I and II, and nearly all those in May in Stages III and IV. Dons (1915) found larvae off northern Norway in April.

*Anapagurus* spp.—Pagurid larvae with three pairs of pleopods in Stage IV have been referred to *Anapagurus*, larvae of *Eupagurus* having four pairs of pleopods. It appears that three species of *Anapagurus* larvae have been taken by the recorder, these being separated most easily, in the crushed state, by the character of the abdomen.

One larva almost certainly belongs to *A. chiroacanthus* (Lilljeborg) described by Sars (1889). In this the spines on the dorsal edge of the 4th and 5th abdominal segments are fairly well marked. The distinguishing character is that there is a pair of ventro-lateral spines on the 5th segment. Two forms found in recorder material are included, one with very small dorsal and ventro-lateral spines and one with somewhat larger spines.

In another larva the dorsal abdominal spines are reduced to minute tubercles and there are no ventro-lateral spines on the 5th segment. This is referred to as *Anapagurus A*. The remaining larva, *Anapagurus B*, also has no ventro-lateral spines, but the dorsal spines are well marked, certainly as distinct as the dorsal spines of *A. chiroacanthus* in the form with larger spines.

Gurney (1942) has illustrated Stage I of *A. hyndmanni* (Thompson) and it would seem that *Anapagurus A* is this species, leaving *Anapagurus B* as *A. laevis* (Thompson). However, the evidence is too scanty to allow positive identification.

The distribution of larvae of *A. chiroacanthus* is shown in Plate XVIII. In 1947 the north-west observations were made in July and October, the Forth observations in October-November; in 1948 the north-west observations were made in July-October, the Forth observations in August-October; in 1949 larvae were obtained in the north-west in September and October, off the Forth in October. The Forth observations follow in succession the north-west observations and the possibility of transportation by currents is raised. It is, however, unlikely that all the larvae on the western side of the North Sea came from the north-west, for larvae were found off the Humber from July to October, 1949. Jorgensen (1923) found larvae quite commonly off Northumberland. The Hull-Rotterdam specimen was found in November, 1949, and the Skagerrak larvae in August, 1948 and 1949.

(Text-fig. 8.) Most larvae occurred in October. The secondary peak of August is due to the occurrence in this month of larvae in the Skagerrak. Thorson (1946) found the larvae from July to October. Most larvae were obtained in 1949, least in 1947.

The distribution of *Anapagurus A* is shown in Plate XVIII. In 1947 the north-west observations were in May to October, off the Forth in November and off the Humber in October. In 1948 the north-west observations were in June to August, off the Forth in August to December and off the Humber in September and October. No larvae were found on the western side of the North Sea in 1949. Here, again, there is an apparent movement southwards of larvae during the autumn.

(Text-fig. 8.) Most larvae were obtained in August, with a secondary peak in November. Very few larvae were found in 1949; most were found in 1948.



Only 3 specimens of *Anapagurus B* were found, all between the Dogger Bank and Danish coast in August, 1948, and June and July, 1949 (Plate XVIII).

*Ebalia* Leach.—Lebour (1928) has described the zoeae of *E. cranchi* Leach and of *E. tuberosa* (Pennant), the former having one tooth at the corner of the telson and the latter three. The larva of *E. tumefacta* (Montagu) has not been described, but an *Ebalia* zoea having two teeth at the telson corner has been obtained in the North Sea. This, presumably, belongs to *E. tumefacta*. The corresponding megalopa has seven spines to the last pleopods as compared with six in *E. cranchi* and four in *E. tuberosa*.

All records of *E. tuberosa* and *E. cranchi* during 1947–49 are shown in Plate XIX. Whilst, generally, both species occurred over the same area, the main concentration of *E. tuberosa* was northerly and of *E. cranchi* off the Humber. Thus, combining the Aberdeen-Lerwick and Leith-Copenhagen lines, there were 26 specimens of *E. tuberosa* and 5 of *E. cranchi* as opposed to 9 and 21 respectively on the combined southern lines. This difference in distribution is in keeping with the fact that *E. tuberosa* is a deeper water species than *E. cranchi*. Only four specimens of *E. tumefacta* were obtained during 1947–49, all on the Aberdeen-Lerwick line (Plate XIX).

(Text-fig. 8.) The peak number of *E. tuberosa* occurred in August, that of *E. cranchi* in October. *E. tumefacta* was obtained in August and September. Lebour (1947) found zoeae of *Ebalia* (mostly *E. tuberosa*) from February to November, chiefly from July to September.

*Hyas* Leach.—(Plate XIX.) The two North Sea species of *Hyas*, *H. coarctatus* Leach and *H. araneus* (L.), were not separated with any real confidence and they must therefore be dealt with together. The main difference shown in Plate XIX is that of the Forth concentration in 1948. Since, however, no Leith-Copenhagen records were obtained when *Hyas* was most abundant (April and May) in both 1947 and 1949 this difference in the charts has no significance.

(Text-fig. 6.) The maximum number occurred in spring. The graphs for the Humber show that the peak number occurred successively earlier each year from 1947 to 1949. Numbers on other lines were too low, or the lines were too inadequately covered, to provide supporting evidence for this feature.

Whilst no larvae were found on the Hull-Copenhagen line or southwards after the end of June, a few scattered specimens were found on the Aberdeen-Lerwick and Leith-Copenhagen lines in July–September.

Jorgensen (1923) found larvae of *H. araneus* only in her earliest samples, in May, and Lebour (1947) says that larvae of *H. coarctatus* are usually seen in early spring. Savage (1926) found only megalopae of *Hyas* in the June–July cruise.

*Corystes cassivelaunus* (Pennant).—(Plate XIX.) The main concentrations of larvae were found on the western side of the southern North Sea, particularly off the Humber. In 1949, in contrast to 1948, larvae were found in the east-central region. On a single record in each year, 1946–1949, larvae were obtained off the Aberdeenshire coast.

(Text-fig. 6.) The highest numbers clearly occurred in spring, April to June. Lebour (1947) recorded larvae from January to June, the largest number seen occurring in March. Savage (1926) found megalopae only in the June–July cruise.

Off the Humber and in the southern North Sea the larvae were much more abundant in 1949 than in 1948. In each year, 1947 to 1949, larvae appeared successively earlier off the Humber and in the Southern Bight; on this point the Bremen line is inconclusive. It is noticeable, too, that the period over which larvae were obtained was much shorter in 1947 than in either 1948 or 1949.

*Portunus* Fabricius.—(Plate XIX.) *Portunus* larvae were not identified to species, since Lebour (1928) states that it is not worth while trying to identify these larvae unless taken alive. Larvae of *Portunus* were markedly predominant over most of the North Sea, and this was especially true in 1949. Few other larvae, apart from *Portunus*, were found over the middle part of the Leith-Copenhagen line.

(Text-fig. 7.) In the north-west most larvae were obtained in 1948 and least in 1949. Off

the Forth 1947 was a poor year. 1947 was also a poor year off the Humber, 1949 being the best year.

On the eastern side of the North Sea the 1947 values are not satisfactory. Larvae were more numerous in 1949 than in 1948 in the east-central region, and this is also probably true for the Skagerrak. Though not shown in the figure, it can be said that larvae on the London-Copenhagen line were also more numerous in 1949 than in 1948. In the southern North Sea no distinct difference between 1948 and 1949 can be ascertained.

The total numbers comprised more than one species; in fact, an impression was gained during analysis that 3 species, at least, contributed substantially to the total. Despite this the various curves show in nearly all cases one distinct peak occurring in July or early August. This implies that the more numerous *Portunus* species have similar hatching times.

*Thia polita* Leach.—(Plate XIX.) Larvae were found only in the Southern Bight.

(Text-fig. 8.) In each year the peak number was obtained in August. Numbers obtained decreased through the period 1947 to 1949.

Lebour (1947) found zoeae in August and September only.

*Atecyclus rotundatus* (Oliv.)—(Plate XIX.) The larvae were found chiefly on the Aberdeen-Lerwick line. Elsewhere they were found only off the Forth, particularly in 1948. Failure to record larvae here in 1949 may well have been due to the short Leith-Copenhagen lines in August and September.

(Text-fig. 6.) An interesting feature are the double peaks, well spaced in time, on the graphs for the north-west in 1948 and 1949; the two curves are sufficiently similar to suggest strongly that this feature is significant. The sequence occurred earlier in 1949 than in 1948. It would seem, too, that it occurred earlier in 1948 than in 1947, certainly in the time of the first appearance of high numbers. A reasonable explanation of the 1947 curve is that the single peak corresponds to the first peaks of 1948 and 1949, and the second peak did not appear.

The peak in numbers off the Forth in 1948 was very pronounced, and it is possible that these were invasion forms from the north-west, where larvae were present in good numbers several weeks earlier.

Lebour (1947) says that larvae are usually found from April to August, the largest numbers in May to July.

*Carcinus maenas* (L.)—(Plate XIX.) Only 5 specimens were obtained, all near the coast in the north-west. They occurred in June and July. Williamson (1903) gives the larval season off Scotland as March to late July.

*Cancer pagurus* L.—(Plate XIX.) Larvae were very common on both sides of the North Sea but not in the Southern Bight.

(Text-fig. 6.) In the north-west it appears that most larvae were present in 1947 and least in 1949. Off the Forth the curves for 1947 and 1948 are very similar to those for *Upogebia deltaura*; the short Leith-Copenhagen records in August and September, 1949, preclude comparable values for this year. The three peak numbers for *C. pagurus* off the Humber, too, occurred at the same time as peak numbers for *Upogebia*. Although it is not quite certain that the peak numbers occurred successively earlier from 1947 to 1949, the appearance of appreciable numbers certainly occurred successively earlier.

There is little acceptable difference between 1948 and 1949, as shown by the remaining graphs for the east-central region, Skagerrak and southern North Sea.

Lebour (1947) found larvae from April to November, the largest numbers in May to July. Thorson (1946) found larvae from mid-May to mid-September. Williamson (1900) says that hatching takes place in July and August.

*Xantho hydrophilus* (Herbst.)—(Plate XIX.) Only 7 larvae were found during 1946–49, in September and October on the western side, in August in the Skagerrak.

*Pilumnus hirtellus* (L.)—(Plate XIX.) Only 19 larvae were found during 1946–49, mainly off the Humber, with an occasional specimen in the Southern Bight in 1946. They occurred



chiefly in August, but were also found in September and October. Lebour (1947) found larvae from May to November, the largest numbers in July.

*Pinnoteres pisum* (L.).—(Plate XIX.) Only two specimens were obtained, one in August and the other in September, 1949.

#### DISCUSSION.

*The relation between the distribution of the adults and their larvae.*—A summary account of the origin and distribution of adult decapods in the North Sea is given by Balss (1926). This is of interest to us since most decapods have larvae which are planktonic for several weeks, and the larval phase must be, and must have been, very important in controlling the distribution and extension of the adults in the North Sea. Balss' account is, consequently, paraphrased below, so that the distribution of the larvae shown in Plates XVII–XIX may be compared with that of the adults. Exact correspondence is not to be expected, since larvae may drift into regions unsuitable for the survival of the adults and thus have a wider distribution. Of the species listed by Balss, as demonstrating each type of distribution, mention is made below only of those species whose larvae enter into this report. In one or two cases there are no examples from recorder material.

According to Balss, then, the North Sea population is of mixed origin with only two endemic species. The remaining species can be divided roughly into two groups: (A) those belonging to the warm water fauna of the Mediterranean and Lusitanian regions and (B) those belonging to the boreal fauna of the North Atlantic.

(A) The warm-water forms penetrate into the North Sea through two routes, shallow water forms through the Channel into the southern North Sea and deeper water forms through the Shetland-Orkney Channel. Three groups can be distinguished of those penetrating through the Channel:

(i) Those that appear only in the most southern part of the North Sea.

(ii) Those that have penetrated further north along the east coast of England. On the east side of the North Sea penetration has not, however, gone beyond latitude 54°, e.g., *Thia polita*, *Pilumnus hirtellus*.

(iii) Those that have penetrated further north on both sides of the North Sea, e.g., *Corystes* (Kattegat, Scotland), *Upogebia stellata* and *U. deltaura* (Moray Firth, Kattegat), *Callianassa stebbingi* (Scotland, Skagerrak), *Galathea squamifera* (Shetland, Kattegat), the three *Ebalia* spp.

Southern forms which have come in through the Shetland-Orkney Channel have expanded towards the south, reaching the east coast of England, but are unknown in the most southern part of the North Sea. Dispersal through their larvae has brought them as far as Norway and the Kattegat. Examples are *Eupagurus prideauxii*, the three species of *Anapagurus*, *Xantho hydrophilus*, *Munida bamfia*, *Atelecyclus*, *Pontophilus spinosus*.

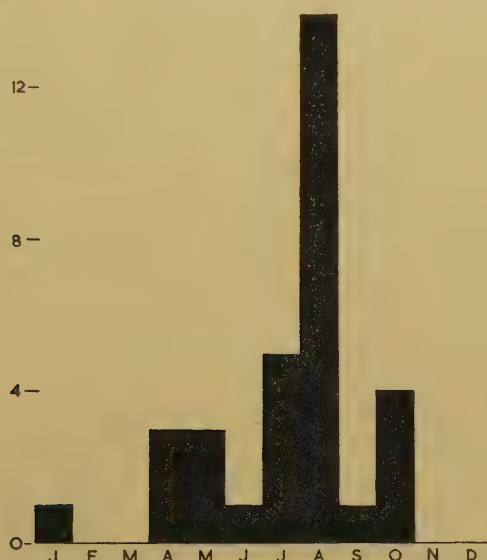
(B) The northern forms have penetrated through the entrance between Shetland and Norway and extended into the Kattegat, to the Dogger Bank and, in part, to the Dutch and south English coasts. Examples are *Eupagurus bernhardus*



and *E. pubescens*, the two *Hyas* spp., *Crangon crangon* and *C. allmanni*, *Pandalus montagui*, *Caridion gordonii* and *Pontophilus hispidus*.

Without going into detail, it can be said that the distribution of the larvae as reported in the earlier part of this report fits in very well with this scheme.

*The reproduction of Decapods.*—Text-fig. 11 shows the number of species, in each month, having the main maximum of larvae in that month. All the species included in Text-figs. 5–8 as well as *Caridion gordonii*, *Processa edulis* and *P. aequimana*, *Callinassa subterranea* (?), *Eupagurus prideauxii* and *E. pubescens*, and *Pilumnus hirtellus* are involved. Some species had their peak number in different



TEXT-FIG. 11.—Histograms showing, in each month, the number of species having their major maximum in numbers in that month.

months in different years and regions, but within the same season (e.g., peak in July or August). A single month has been assigned to each species, that month which had the peak numbers most commonly. The selection of an alternative month would make no difference to the consideration which follows.

The species fall into two groups, those with the main hatching in spring and those with the main hatching in summer and autumn. *Crangon crangon* had its main peak in January (Text-fig. 8), due to an unusually high number off the Dutch coast in January, 1948. Since there was also a peak number in April this species is taken as belonging to the spring group. The highest number of *Crangon allmanni* was obtained in June but, as Text-fig. 8 shows, the species undoubtedly belongs to the spring group.

Balss (1926) distinguished only between warm water and boreal, or northern, forms. Wedermeyer (1913) and Blohm (1915) separated the species into more zoogeographic categories and distinguished an arctic zone, a boreo-arctic zone

(Blohm only) from the boreal and warmer zones. Of the eight species, included in Text-fig. 11, with the main hatching in spring, six are found in the arctic zone and one in the boreo-arctic zone (*Munida bamffia*), according to the tables of Wedermeyer and Blohm. The only species with the main hatching in spring which does not extend into colder water than the boreal zone is *Corystes cassivelaunus*. With the exception of *Pontophilus bispinosus* all the species included in Text-fig. 11 with the main hatching in summer and autumn do not extend into colder water than the boreal zone.

Despite the exceptions it seems a general rule from the present results that species extending north of the boreal zone have their main hatching in spring in the North Sea, whilst species extending no further north than the boreal zone have their main hatching in summer or autumn. Balss (1926) makes a similar point in that, generally, northern forms are in berry in winter, southern forms in summer. He recognizes that there are many exceptions to this rule, as there must be in view of the fact that many species are in berry for a long period (e.g., *Homarus vulgaris* 11–12 months, *Nephrops norvegicus* 9 months).

It is interesting to note the comparative success in the southern North Sea of the larvae of some northern species which have their main hatching in spring. Thus the larvae of *Eupagurus bernhardus* were found much more commonly over the Dogger Bank than elsewhere. Both species of *Crangon* were found more commonly in the south than in the north. Taking contrasting species, the larvae of the warm water *Pandalina brevirostris* had a more northerly distribution than those of the northern *Pandalus montagui*. It is not surprising that *E. bernhardus* and the *Crangon* species breed successfully in the southern North Sea. Referring, again, to the tables of Wedermeyer and Blohm, it is clear that the temperature tolerance of these northern species includes temperatures of the arctic to boreal zones, the warm water species the boreal to Mediterranean zones. Generally speaking, the bottom water of the southern North Sea becomes colder in winter than the northern deeper water (see Anon, 1927). Northern forms would find the low temperatures of winter in the south favourable, whereas the southern forms would find these temperatures, at least less favourable, even if not adverse. Conversely, a warm-water species might find the all-the-year-round conditions more favourable in the north than in the south. For example, the main breeding population of *Atelecyclus*, though a warm-water species, must be restricted to the north-west of the regions covered by the recorder, since larvae were found no further south than the Forth, and may even have arrived here as a result of transportation from the north.

Whilst the reproductive habit is fairly well known in some decapods of direct commercial value (e.g., *Cancer pagurus*, *Crangon crangon*, *Leander*) little is known about the great majority of decapods, though these are of immense indirect commercial importance as food for demersal fish. Decapods, with the exception of the Penaeidea, of which no larvae were found, carry their eggs between spawning and hatching. This egg-carrying period varies considerably between species (e.g.,



7–8 months in *Cancer pagurus*, 35–40 days in *Leander squilla*) ; it also varies within a species according to season, e.g., *Crangon crangon* (Lloyd and Yonge, 1947, fig. 12). It does not seem profitable at present to attempt to explain why larvae were more frequent or appeared earlier in one year than another. The abundance and appearance of larvae may be dependent on factors acting on the adults before spawning, or on the spawn during the egg-carrying period, or on the newly-hatched larvae. Difficulty arises because the occurrence of larvae is insufficient indication of spawning time ; the duration of egg-carrying is unknown in most species.

The general scarcity of decapod larvae in 1947 (Text-fig. 4) may, however, have arisen through the unusual temperatures prevailing at the bottom in this year, or both features may be related to the unusually weak oceanic influx into the North Sea up to September or October (Tait, 1949). Whilst surface waters became much warmer than the average around July–October (Smed, 1949), the bottom waters remained abnormally cold throughout the year in the northern half of the North Sea (Tait, 1949). Thomsen (1949) recorded large negative temperature anomalies at the light-vessel “ Vyl ” from April to August, 1947.

It may be possible to go a stage further and relate the trends shown by some species to the unusually low bottom temperature of 1947.

In the north-west the two hatchings of *Galathea dispersa* in 1947 occurred a month later than in 1948 and 1949 (p. 171). *Atelecychus* apparently had two hatching periods in 1948 and 1949 and only one in 1947. This single hatching was interpreted as a late first hatching (p. 175), the season then being too far advanced for the second hatching to appear. Both these species are warm-water forms. Most specimens of the northern forms *Caridion gordonii* (p. 166) and *Munida* (p. 172) were obtained in 1947.

The northern form *Eupagurus bernhardus* was certainly most abundant around the Dogger Bank in 1947. The graphs for the Humber (Text-fig. 6) suggest that its increase in numbers was later in 1947 than in the following years, but this is doubtful, since there was no record between March 22nd and May 18th.

There are several other examples where it might be reasonable to relate trend and temperature, but information on the biology of decapods is so limited that one must be chary of developing the matter further.

*The larval population in the regions.*—In the foregoing part of this report the species have been presented separately, and it is not easy to appreciate the nature of the population in the different regions from these accounts. One way of defining a population is to list the dominant species as assessed by the percentage composition of the total decapod larval population. This is shown in Table I, species exceeding 5% of the total population taken throughout 1947–49 being distinguished as the dominant species. The total numbers, on which the percentages are based, are also given. It is, of course, obvious that the percentage composition of the larvae is no measure of the percentage composition of the adults.

Particular mention may be made of the high percentage of *Portunus* larvae. Larvae of at least six different species may be present in the generic group and,



therefore, the larvae of individual species of *Portunus* may have been hardly more common than those of *Upogebia deltaura*, *Cancer pagurus*, etc.

TABLE I.—Showing the Percentages of Various Species in Total Decapod Larvae obtained throughout 1947–49 in the Separate Regions (Text-fig. 1) and over the whole North Sea (NS). Values over 5% are shown in heavy type. The total numbers are also given.

|                                  | NW.  | F.  | H.   | SNS. | SB. | EC. | Sk. | NS.    |
|----------------------------------|------|-----|------|------|-----|-----|-----|--------|
| <i>Orangon crangon</i>           | +    | +   | +    | +    | 11  | +   | +   | +      |
| <i>C. allmanni</i>               | 1    | +   | +    | 1    | 5   | +   | +   | +      |
| <i>Pontophilus bispinosus</i>    | +    | 2   | 1    | 6    | 0   | 4   | +   | 2      |
| <i>Upogebia deltaura</i>         | 6    | 4   | 8    | 25   | +   | 5   | 4   | 9      |
| <i>Callianassa stebbingi</i> (?) | 4    | 3   | 8    | 13   | 3   | 4   | 1   | 7      |
| <i>Galathea dispersa</i>         | 11   | 4   | +    | +    | 0   | 3   | 3   | 2      |
| <i>G. intermedia</i>             | 2    | 6   | 2    | +    | +   | 1   | +   | 2      |
| <i>Porcellana longicornis</i>    | 3    | +   | 4    | 2    | 10  | 0   | +   | 3      |
| <i>Eupagurus bernhardus</i>      | 2    | 5   | 14   | 2    | 4   | 14  | 4   | 8      |
| <i>Hyas</i> spp.                 | 3    | 6   | 3    | +    | 1   | 2   | 4   | 3      |
| <i>Portunus</i> spp.             | 13   | 35  | 39   | 33   | 33  | 52  | 62  | 38     |
| <i>Atelecyclus rotundatus</i>    | 15   | 8   | 0    | 0    | 0   | 0   | 0   | 2      |
| <i>Cancer pagurus</i>            | 18   | 8   | 6    | 3    | +   | 14  | 13  | 8      |
| Total numbers of larvae          | 1380 | 850 | 3880 | 2010 | 770 | 880 | 580 | 12,300 |

Considering, very briefly, each region in turn, and taking all results into account, very few of the common species were found most frequently in the north-west and only *Galathea dispersa* and *Atelecyclus* can be singled out. Several of the uncommon species, however, occurred most frequently here: *Caridion gordonii*, *Munida*, *Eupagurus prideauxii*, *Ebalia tumefacta* and, near the Shetlands, *Galathea squamifera*.

There is considerable circumstantial evidence that many larvae arrived off the Forth from the north. Thus in 1947 *Galathea dispersa* and *Cancer pagurus* first appeared in the collections in October and *Upogebia deltaura* in November, after late hatchings in the north-west (Text-figs. 5 and 6). Hatchings were earlier in 1948–49 and invading larvae cannot be distinguished from larvae derived locally. Furthermore, larvae of *Eupagurus prideauxii*, *Anapagurus chrioacanthus* and *Anapagurus A* were found some time later off the Forth than in the north-west (pp. 172–3). It is not possible to estimate how much of the Forth population arrived from the north; the species listed appeared rather late at the Forth, in October to December, when the decapod larvae had generally greatly decreased in numbers (Text-fig. 4). The possibility that *Atelecyclus*, *Cancer pagurus* and other larvae arrived earlier in the year in 1948 and 1949 cannot, however, be excluded. This is particularly so in 1949, when the main autumn influx occurred unusually early, in August (Tait, 1950).

Off the Humber appreciable numbers of *Hyas*, *Corystes*, *Callianassa stebbingi* (?), *Upogebia deltaura* and *Cancer pagurus* appeared successively earlier from 1947 to 1949. In the earlier part of the text some caution was exercised regarding *U*,

*deltaura* but, with these other examples, it is fair to accept this feature for the species. The factors which caused this succession operated on species whose main hatchings were spread over three months or so; the lateness in 1947 may be related to the temperature conditions.

The population in the Southern Bight was rather variable from year to year. Thus, in successive years, the percentages for *Crangon crangon* were 8%, 20%, 1%, for *C. allmanni* 14%, 10% and 0%, and for *Porcellana longicornis* 0%, 5%, 33%. Only in this area were larvae of *Thia polita* and *Callianassa subterranea* (?) found.

The percentage composition of the populations in the east-central and Skagerrak regions (Table I) was very similar, particularly in the high values for *Portunus*. The main difference lies in those for *Eupagurus bernhardus*, but this arises because part of the Dogger Bank is included in the east-central region. The high percentage of this species at the Humber is similarly explained. Since the Humber and east-central regions were sampled by the same recorder line, it is possible to compare the time of occurrence of peak numbers with reference only to the dates of peaks. The east-central region had peak numbers in 1948 and 1949 later than those at the Humber of *Pontophilus hispidus*, *Upogebia deltaura*, *Callianassa stebbingi* (?), *Eupagurus bernhardus* and *Cancer pagurus*.

As a final comment it may be said that very few larvae of truly intertidal decapods were taken (e.g., *Carcinus maenas*), and nothing exactly comparable to the extensive off-shore dispersal of such larvae as *Emerita analoga* has been found (Johnson, 1939). However, a similar effect of off-shore dispersal is probably shown by the larvae of *Cancer pagurus* (Plate XIX). Pearson (1908) and many other workers have referred to the breeding migration of this crab. The mature adults spend the winter in off-shore water of 20–30 fms. depth and in spring migrate towards the shallow water of the shore to hatch around July.

#### SUMMARY.

1. At 10 m. the main concentrations of decapod larvae occurred south of the Dogger Bank, from the Humber into the Heligoland Bight. The larvae were present in greatest numbers in July and August, and there was a small but consistent peak in numbers in April–May.

2. The larval distributions and seasons of 41 species (and occasionally genera) are given.

3. The distributions of larvae agree well with the accepted views on the distribution and origin of adult decapods in the North Sea.

4. As a general rule species with an adult extension north of the boreal zone have their main hatching in spring, and species not extending so far have their main hatching in summer in the North Sea.

5. Some northern species breed more successfully in the south than in the north of the North Sea and vice versa for southern species. This is explained by the lower temperature of bottom water in the southern North Sea in winter.

6. There is considerable circumstantial evidence that many larvae arrived at the Forth from the north.

7. It is suggested that the trends shown by total decapod larvae and of some species were related to the unusual temperature conditions prevailing in 1947.

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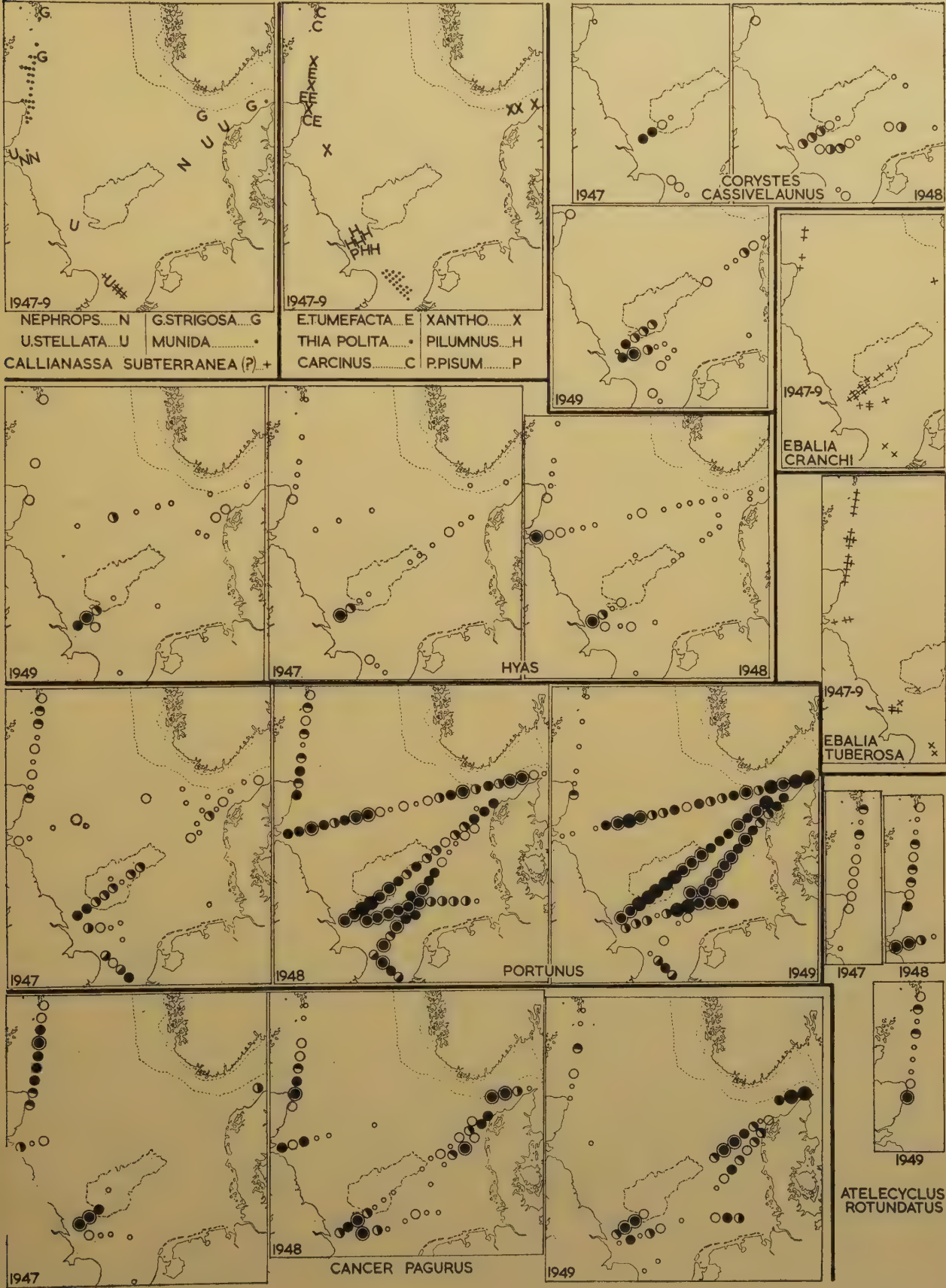
#### EXPLANATION OF PLATES.

Charts showing the distribution of larvae of species or genera, either for the period 1947-49 or for each year separately. There are two types of charts: (a) all 10-mile samples on which larvae were found, irrespective of number, are indicated, usually by + ; (b) the highest number of larvae obtained on each 20-mile unit (two adjacent 10-mile samples) throughout the period is shown by a symbol, in accordance with the range scale given on Plate XVII.













# CONTINUOUS PLANKTON RECORDS: THE EUPHAUSIACEA OF THE NORTH-EASTERN ATLANTIC AND THE NORTH SEA, 1946-1948.

BY

R. S. GLOVER, B.Sc.

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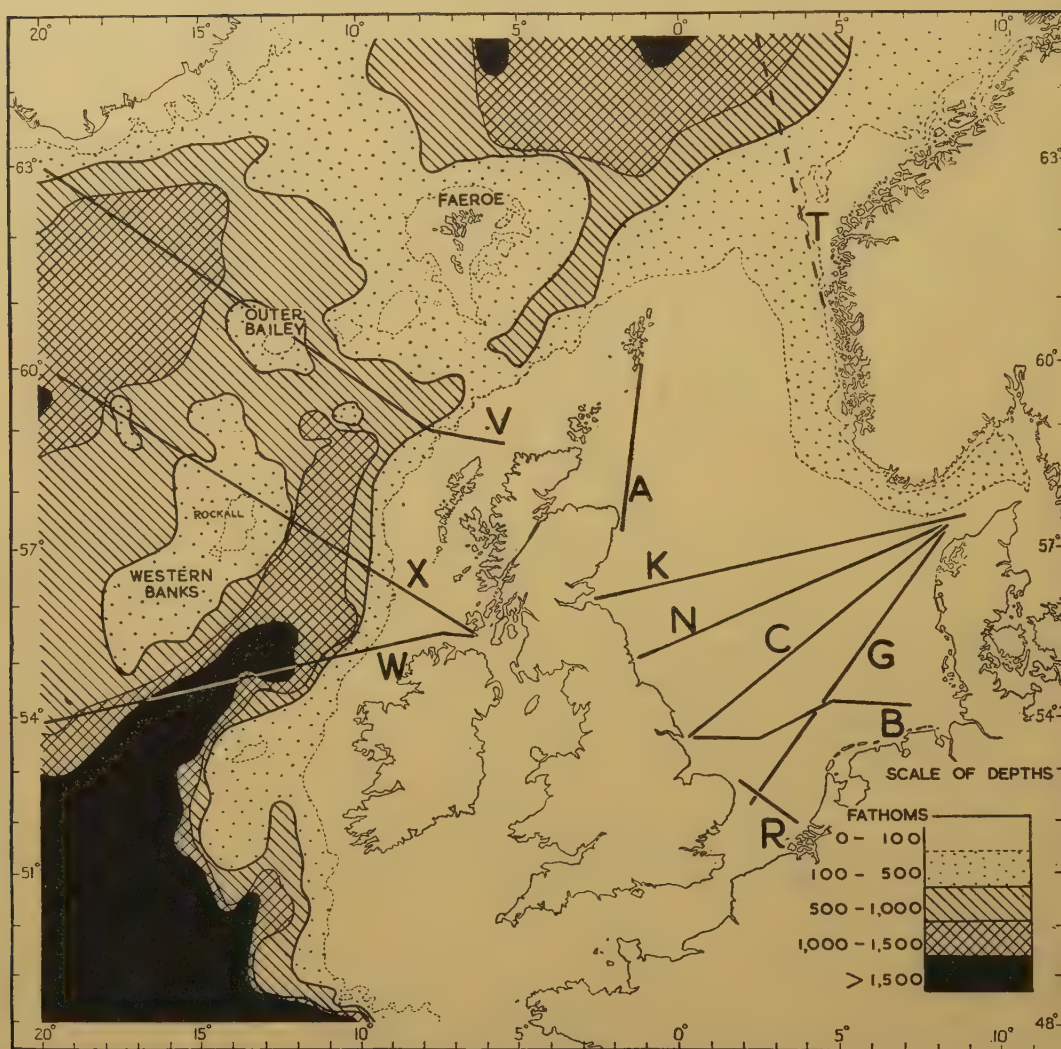
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## INTRODUCTION AND METHODS.

This paper is a continuation of the work of Marshall on the euphausiids taken by the Continuous Plankton Recorder in the North Sea and Atlantic (Lucas, Marshall and Rees, 1942, and Marshall, 1948). Hardy (1939 and 1941) and Rae (1952) have described the techniques and methods involved in Recorder sampling.

Text-fig. 1 illustrates the routes which are used and the depth of the water. The Recorder samples are all taken 10 metres below the surface. This account deals with records from the North Sea and the Pentland-Iceland route in 1946 and 1947, and from these and the "W" and "X" records in 1948. Since 1948 the author's time has become increasingly occupied by work on the relationship between the herring and plankton, and for this reason it has been thought advisable to publish these results in their present form, although it would have been desirable to include data from at least one more year in the Atlantic.



TEXT-FIG. 1.—Chart showing the Continuous Plankton Recorder routes from which the euphausiids were taken. Routes 'A,' 'K,' 'C,' 'B,' 'R' and 'V' were started during 1946, 'G,' 'N' and 'W' became available in November 1947 and the 'X' route in January 1948. The 'T' route, shown as a broken line, was started in January 1949 after the period covered by the present paper (see text p. 189). For details of the month-by-month sampling see Rae (1952).

During 1946 each species was divided into "adults" and "larvae" using the rough criteria employed by Marshall (1948) (i.e., the presence or absence of the adult form of telson and antennae), but it was decided that this had the disadvantage of cloaking a developmental stage which could be fairly easily defined in the Recorder material. In 1947 and 1948, therefore, the results were expressed as adults, cyrtopia, and furcilia.<sup>1</sup> Both Fraser (1936) and Einarsson (1945) have

<sup>1</sup> Calyptopis stages were very rare in the material, and nauplii were grouped with other crustacean nauplii. For these reasons reference to these two stages is omitted.

criticized the practice of categorizing the young forms as furcilia and cyrtopia, terms introduced by Sars (1885). Their arguments are based on the lack of significance of these categories but, from the ecologists' point of view, Sars' stages have the considerable merit that they can be easily recognized, and that they make possible a rough division into young, adolescent and adult animals. The precise significance of the terms furcilia, cyrtopia and adult must vary from species to species because of differing life-histories, but they form rough guides to development in a study of the present kind. It was usually possible to distinguish between furcilia and cyrtopia on the basis of development of the antennular flagellum, but the distinction between cyrtopia and adult was more variable, being largely dependent on the form of the telson. For some purposes these two stages are combined with the intention of distinguishing young forms (furcilia) from older forms (adults and cyrtopia). It should perhaps, be emphasized that Marshall (1948) combined furcilia and cyrtopia stages as "larvae," whilst those forms referred to as adolescents by Einarsson are probably often described as adults in the present paper.

Identification was based on the descriptions and keys to be found in Sars (1885), Lebour (1925), Frost (1934, 1935) and Einarsson (1945).

Rae (1952) has described the reduction in the analysis of Recorder material after 1947, which involved the omission of alternate 10-mile blocks. In 1946 and 1947 all euphausiids were identified on every block, but in 1948 only alternate blocks were analysed; this is equivalent to studying one sample collected over 10 miles and representing about  $3.0 \text{ m}^3$  of water in every 20 miles of record. In order to facilitate comparison with other work the results are here expressed as the number of euphausiids per  $10 \text{ m}^3$  of water sampled.

Recorder samples, taken from a uniform depth of 10 m, require careful interpretation in the light of the diurnal migrations of zooplankton. Marshall (1948, pp. 181, 182) discussed this problem in relation to the euphausiids, which generally make extensive vertical migrations. The necessity for caution has been borne in mind throughout the present paper but, to enable the reader to appreciate first the nature of the material, discussion of vertical migration is deferred to p. 210.

#### DISTRIBUTION OF THE EUPHAUSIACEA.

The following eight species were recognized:—

|                                            |                                           |
|--------------------------------------------|-------------------------------------------|
| <i>Euphausia krohnii</i> (Brandt),         | <i>Thysanoessa longicaudata</i> (Krøyer), |
| <i>Nematoscelis megalops</i> G. O. Sars,   | <i>Thysanoessa inermis</i> (Krøyer),      |
| <i>Stylocheiron longicorne</i> G. O. Sars, | <i>Thysanoessa raschii</i> (M. Sars),     |
| <i>Meganctiphanes norvegica</i> (M. Sars), | <i>Nyctiphanes couchii</i> (Bell).        |

Text-figs. 2, 3, 10 and 11 show their distributions. In Text-figs. 2 and 3 the area sampled has been divided into squares, each of which corresponds to four of the standard international squares. Symbols in each square denote the average number of furcilia, cyrtopia and adults per  $10 \text{ m}^3$  sampled during the 12 months





TEXT-FIG. 2.—Charts showing the average numbers per 10 m<sup>3</sup> of water sampled, of 5 euphausiid species taken by the Recorder during the 12 months, January to December 1948. Each square represents 4 of the standard international squares, a reference to which is shown in the chart for *Meganyctiphanes norvegica*. The total number of Recorder blocks analysed is shown in the top left-hand corner of each square; each block represents a 10-mile sample equivalent to 3.0 m<sup>3</sup> of water filtered.

January to December, 1948. The number of 10-mile blocks which were analysed from each square is also shown. Some squares were very heavily sampled throughout the period, whilst others represent only a small number of Recorder blocks. This inequality of sampling necessitates caution in applying detailed quantitative treatment; only restricted use can be made of the poorly sampled squares.

The species group into three types of distribution, each corresponding to characteristic depths of water above which the records were taken. This apparent correlation between depth and specific distributions is illustrated in Text-figs. 10 and 11, where the records in the Atlantic are shown with the depths of water. Whilst it is convenient to use these characteristic depths in describing the three types of distribution this does not necessarily imply that depth is suggested as the limiting factor. Bottom configurations and water movements are variably inter-related and have their effects on the character of the water, as measured for instance by temperature and salinity. These features of the environment are referred to in the present paper but it is not possible to assert that one or the other is decisive in determining the distributional types, which may be characterised as—

- i. Oceanic deep-water species.
- ii. Oceanic species with a wide distribution.
- iii. Shallow water species.

It should be emphasized that these depth distinctions refer to the location in which the euphausiids were captured by the Recorder at 10 metres below the surface.

*Oceanic deep-water species.*

*E. krohnii* and *N. megalops* (Text-figs. 2 and 11) were found only to the west of the Continental Slope and usually over water of more than 500 fathoms depth.<sup>1</sup>

Their greatest concentration lay to the south of the area, over water deeper than 1500 fathoms. Although some 80 Recorder blocks were taken at all times of the year over the Western Banks (including Rockall), neither of these species was found there. Text-figs. 2 and 11 show that their distribution very closely followed the configuration of the deep water which runs as a wide channel from the very deep Atlantic in the south, narrows between the Western Banks and the Continental Shelf and ends near the Wyville-Thompson Ridge. Beyond this ridge these species were found only over the deep between the Faeroes and Shetlands, and over the deep water off Norway (on the first record from Bergen to Weather Station "M" in January, 1949). Although this latter record is outside the dates of the present survey, it is worth recording here that the area of distribution of these forms extends so far north.<sup>2</sup>

<sup>1</sup> *Stylocheiron longicorne* probably falls into this category although it was only found once, in May, 1948, when a single cyrtopia stage appeared over deep water to the west of Northern Ireland. Its position is indicated in Text-fig. 2 by the symbol S.

<sup>2</sup> Boldovskii (1937) describes three captures of *N. megalops* off the North Cape, in latitude 71° N.; more recently Mr. J. Corlett of the Ministry of Agriculture and Fisheries (Lowestoft), in a private communication, reported this euphausiid at 70° N., 14° E., and even further north at 74° N., 19° E., during the winter of 1950-51.



This distribution is in conformity with that described by Einarsson (1945), by Fraser and Saville (1949), by Fraser (1950), and by Marshall in Lucas, Marshall and Rees (1942).<sup>1</sup> Such a distribution, providing strong similarities with the depth contours, is also in close agreement with the known currents in the eastern Atlantic. Hermann and Thomsen (1946, text-fig. 26) show two northbound Atlantic currents, one of which, immediately to the east of the Western Banks, corresponds closely with the distribution of *E. krohnii* and *N. megalops*; the other is well to the west of the Bank, in the vicinity of longitude 25° W., and outside the area of the present survey. The distribution of these species accords with the work of Helland-Hansen (1930, 1936) as reported by Sverdrup *et al.* (1942), and of Hermann and Thomsen, who showed that Atlantic water flows into the Norwegian Sea mostly between the Faeroes and Shetlands, whilst Arctic water flows out between Iceland and Greenland.

These observations suggest the arrival of *E. krohnii* and *N. megalops* from the south of the area investigated. In the present material adults and cyrtopia appeared in July–August, reached a maximum in November and December, and had disappeared by February; there were very few furcilia stages, but some of these may have been overlooked amongst the large numbers of *Thysanoessa* larvae. Einarsson (1945) found “juvs” at the edge of the deep Faeroe-Shetland trough.

It is possible that these oceanic species will prove to be useful in tracing water movement from the eastern Atlantic, across the Wyville-Thompson Ridge and into the Norwegian Sea. *Euphausia krohnii* has apparently never been recorded in the North Sea but *N. megalops* was reported there by various workers off the east coasts of Scotland, Northumberland, Durham and Yorkshire (Norman, 1892, and Norman and Brady, 1908), and by Marshall (1948) off Aberdeenshire in February of both 1938 and 1939. Since its period of maximum abundance in the Atlantic was found to be November and December of 1947 and 1948 and it was detected off the Norwegian coast in January, 1949, it is perhaps less surprising than Marshall inferred that it should be found in the North Sea in February as an indicator of the flow of warm Atlantic water into the North Sea.

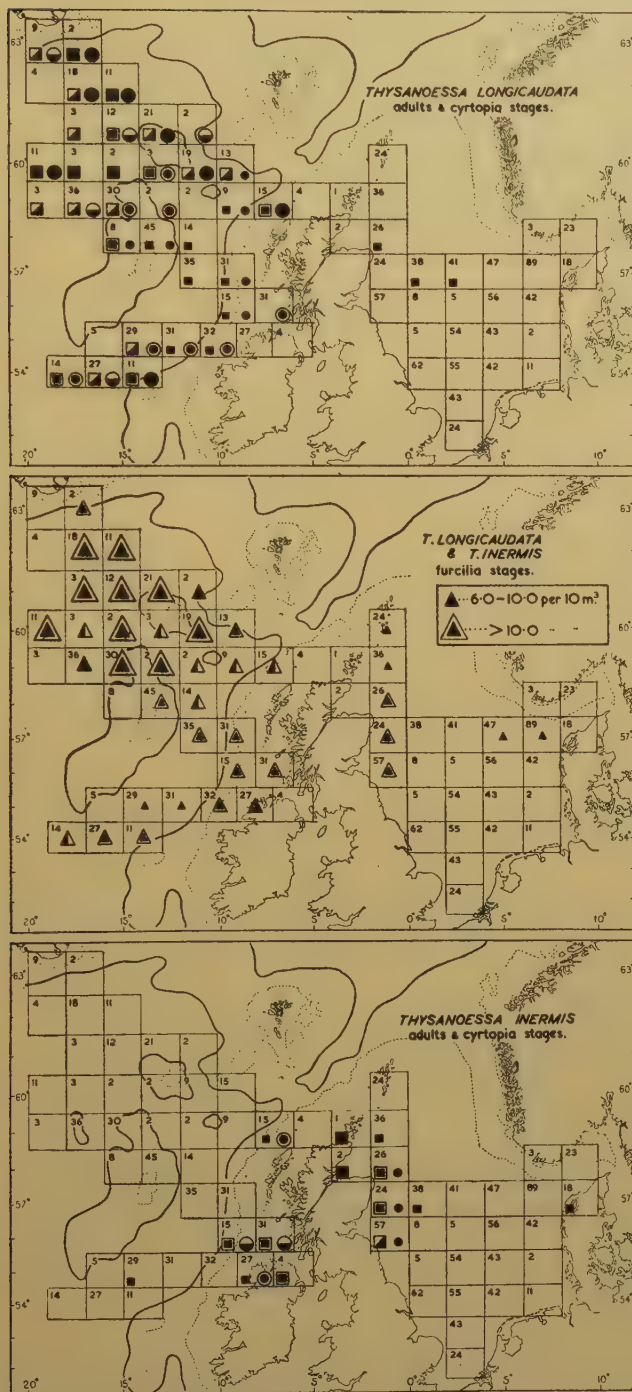
#### *Oceanic species with a wide distribution.*

These are defined as species whose major concentrations occurred in oceanic waters with a depth of over 500 fathoms, and were also found less commonly over shallower waters. *Meganyctiphanes norvegica* and *Thysanoessa longicaudata*, the members of this group, have been found everywhere in the Atlantic area investigated,

<sup>1</sup> I have re-examined most of the material from the Pentland-Iceland Records described by Marshall in Lucas, Marshall and Rees (1942) and I am satisfied that most, if not all, of the specimens allocated there to *T. raschii* are in fact *T. longicaudata*. Whilst the majority of the *Meganyctiphanes* described by Marshall are undoubtedly of that species, I have detected one adult specimen of *E. krohnii*, in August, 1939, on Record 6V, block 15; this is indicated on Text-fig. 2.

I am indebted to Mr. Marshall for confirmation of this new assessment of the pre-war collections.—  
R, S, G,





TEXT-FIG. 3.—Charts showing the average numbers of adults and cyrtopia stages of *Thysanoessa longicaudata* and *T. inermis* and of the combined furcilia of the two species taken by the Recorder during 1948. Scale and symbols as in Fig. 2, with the additions shown in the inset for furcilia stages.

whereas the first group of oceanic species were confined to a relatively narrow band of deep water.

Text-figs. 2 and 3 show that the densest concentrations of *Meganyctiphanes* and *T. longicaudata* lay to the north and west of those of *Nematoscelis* and *E. krohnii*, and that, unlike these last two, they were common over the Western Banks. In addition, as Marshall (1948) also found, *Meganyctiphanes* was regularly present in the Skagerrak and off the Norwegian coast, but only over the deep water there; it also occurred less regularly in the western North Sea, although it was never found south of the Northumberland coast. It was found in the north-western North Sea in January, February and August of 1947 but never in 1948.

*T. longicaudata* has similarly occurred occasionally in the north-western North Sea, for example in July and December, 1948 (Text-fig. 3), and as far south as the Dogger, in March, 1947. The erratic appearance of both these species in the north-western North Sea may be linked with their major distribution in the Atlantic, since those parts of the North Sea in which they were found are roughly the "elegans" area of Russell (1939, fig. 5) or the oceanic and mixed water of Fraser (1939), which are presumed to be related to the Atlantic inflow into the North Sea.

Text-fig. 4, shows, month by month, the average number

of *Meganyctiphanes* and *T. longicaudata* per 10 m<sup>3</sup> of water sampled to the west of the 500 fathoms contour on the Continental Shelf, their main area of distribution.<sup>1</sup> Furcilia stages of both species were more numerous by day than by night; this was also true of the other stages of *T. longicaudata*, but the reverse appears to apply in the example of *Meganyctiphanes*, of which less than half as many adults and cyrtopia were taken by day as by night.<sup>2</sup> This is illustrated in Table I.

TABLE I.—Captures of *T. longicaudata* and *M. norvegica* during 14 months of Atlantic sampling.

| Species.               | Total number captured. |           |           | Average number per 10 m <sup>3</sup> . |           |           | Ratio $\frac{\text{Day}}{\text{Night}}$ . |           |           |     |
|------------------------|------------------------|-----------|-----------|----------------------------------------|-----------|-----------|-------------------------------------------|-----------|-----------|-----|
|                        | Adults.                | Cyrtopia. | Furcilia. | Adults.                                | Cyrtopia. | Furcilia. | Adults.                                   | Cyrtopia. | Furcilia. |     |
| <i>T. longicaudata</i> | . Day .                | 310       | 553       | 963                                    | . 4.5     | 8.0       | 14.0                                      | . 2.0     | 8.0       | 3.9 |
|                        | Night .                | 197       | 88        | 318                                    | . 2.2     | 1.0       | 3.6                                       | . —       | —         | —   |
| <i>M. norvegica</i>    | . Day .                | 15        | 1         | 174                                    | . 0.2     | (0.01)    | 2.5                                       | . 0.4     | —         | 6.2 |
|                        | Night .                | 44        | 4         | 37                                     | . 0.5     | (0.05)    | 0.4                                       | . —       | —         | —   |

293 blocks representing 880 m<sup>3</sup> were analysed from night sampling, and 230 representing 690 m<sup>3</sup> from daylight sampling.

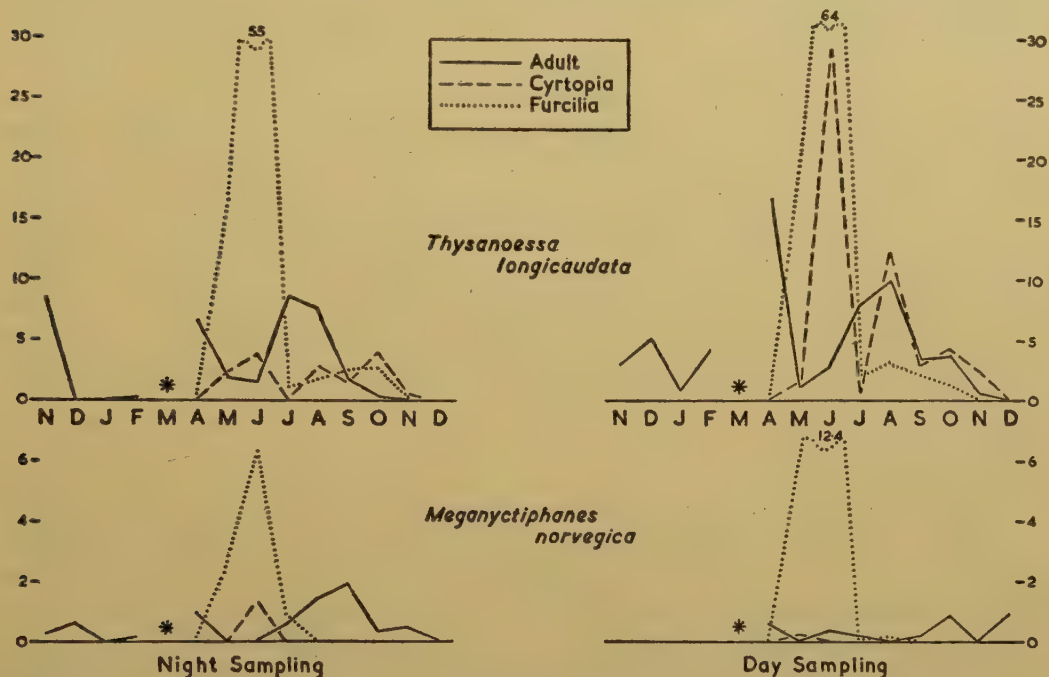
Text-fig. 4 shows a similar annual cycle for both species; the difference in the scale of plotting reduces the marked dominance of *T. longicaudata*. An increase in the number of adults at 10 metres may have occurred in March but was certainly apparent in April, and was followed in May and June by very high numbers of furcilia, the greatest concentrations occurring on the "V" route, where *T. longicaudata* reached 100 and *Meganyctiphanes* some 20 per 10 m<sup>3</sup>. The maximum numbers of cyrtopia occurred about a month after the first furcilia appeared, and it is noticeable that whilst both these young stages of *Meganyctiphanes* were present for a very short time, those of *T. longicaudata* persisted for some six months at the Recorder sampling depth. The spermatophores of the latter species, which were far more common than those of any other euphausiid, were similarly found for some 6 months, from April to September (Text-fig. 10). After a decline during mid-summer the numbers of adults of both species increased in July or August (Text-fig. 4). Einarsson's (1945) measurements suggest that both species reach

<sup>1</sup> Both in order to save time and because of the somewhat squashed nature of Recorder material, the furcilia stages of *T. longicaudata* and *T. inermis* have not been identified separately. This creates difficulties in the detailed interpretation of the life-histories of the two, but the absence of adults of *T. inermis* over deep oceanic water and the scarcity of *T. longicaudata* in Shelf water and in the North Sea suggest that most *Thysanoessa* furcilia found west of the Continental Slope are of *longicaudata*, and the majority of those found inside the 100-fathom contour are likely to be *inermis*.

<sup>2</sup> For convenience the limits of night and day were taken as sunset and sunrise (see Rae, 1952).

adult form in August or September, some 3–5 months after their appearance as larvae; it appears likely, therefore, that this second adult peak in the Recorder material represents the O-group of adults developed from the spring spawning some 3–5 months earlier.

Furcilia stages of *Meganyctiphanes* were also found in the Skagerrak but not until July, 1947, or August, 1948, some 3 months later than in Atlantic waters. The numbers do not warrant a similar graphical treatment to that applied to the



TEXT-FIG. 4.—Graphs showing the average numbers, by day and by night, of *T. longicaudata* and *Meganyctiphanes*, from November 1947 to December 1948 on those parts of the 'W,' 'X' and 'V' records in the Atlantic which were to the west of the Continental Slope, defined by the 500-fathom contour. The vertical scale gives numbers of euphausiids per 10 m³ of water sampled. An asterisk indicates that no information is available.

Atlantic data in Text-fig. 4; this probably reflects the fact that only a small proportion of Recorder sampling in the Skagerrak was over the deep water off the Norwegian coast which *Meganyctiphanes* appears to inhabit.

Text-figs. 2 and 3 show that whilst all stages of *T. longicaudata* were common over the deepest water (in the south of the area sampled, on the "W" route), only a few *Meganyctiphanes* were found there and these were adults. Einarsson (1945) found that the latter species, whilst scarce in shallow regions, was rare in very great depths. The present material confirms this tendency, and suggests that the main areas of distribution of *Meganyctiphanes* are restricted to localities with a depth of between 500 and 1500 fathoms. *Thysanoessa longicaudata* was



rare in shallow waters but seemed to be subject to no limitation in areas of very great depth; Einarsson gives evidence of its great depth range, and comments that it would not be surprising to find that it prefers great depths in the winter and rises to the upper strata immediately before spawning. The Recorder data show that the sharpest distinction between summer abundance and winter scarcity of this species occurred on the "W" records, where the depths run to 2000 fathoms; the distinction was less marked on the "X" route with depths down to 1500, and was least evident on the "V" records with maximum depths of 700 fathoms.

It is, of course, not new to find that the distribution of an animal is limited by its depth requirements for "over-wintering"; Russell (1936) stressed this point, using three examples. Sømme (1934) had shown that *Calanus hyperboreus* requires the deepest water for winter survival whilst *C. finmarchicus* can find suitable depths in coastal waters, and Kramp (1927) thought the shallowness of the Belt Sea was the main factor which made this area unsuitable for *Aglantha*. This kind of depth limitation probably applies to *T. longicaudata* and *Meganyctiphanes*, which were both found over Atlantic Shelf water in summer but not in winter. This is shown in Text-fig. 10, where *T. longicaudata* is seen to have shifted eastwards towards coastal waters from January to May and westwards and oceanwards from June to December; the similar movement of *Meganyctiphanes* is shown in Text-fig. 11.

#### *Shallow-water species.*

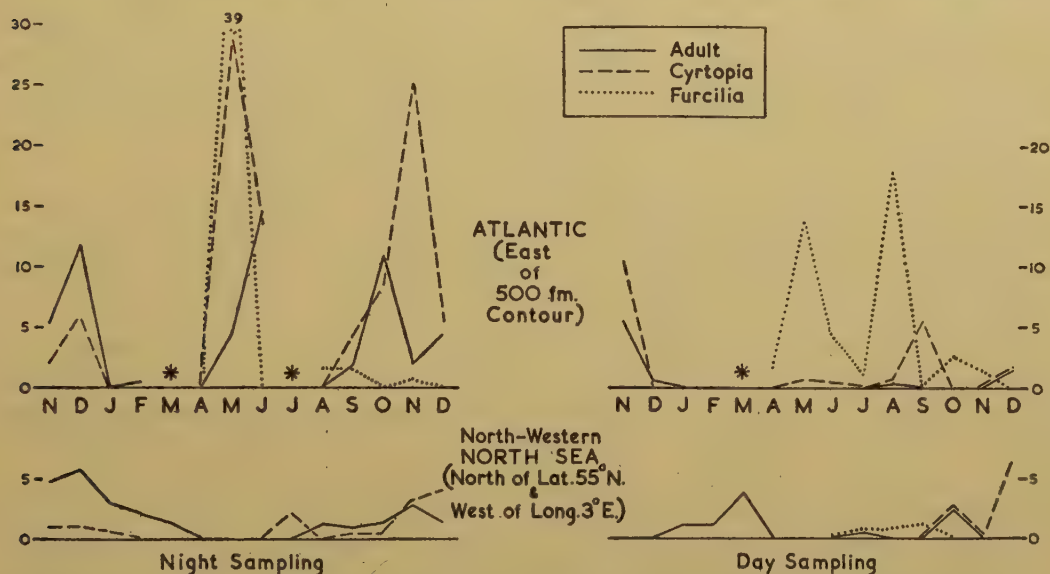
These are defined as those species which were normally confined to waters with a depth of less than 100 fathoms, and which were extremely rare above depths greater than 500 fathoms. In the present work three species have conformed to this definition—*Nyctiphanes couchii*, *Thysanoessa inermis* and *T. raschii*.

Marshall (1948) regarded these three as being characteristic North Sea forms, *Nyctiphanes* being considered ubiquitous but with its densest concentrations in the north-west, *T. inermis* almost solely north-western and *T. raschii* a north-eastern species. The present material fits these descriptions, and adds information concerning the Atlantic distribution.

The investigations of the International Council in 1902–1908 showed that *Nyctiphanes* was abundant in the Bay of Biscay and the English Channel, but that it penetrated only into the southernmost part of the North Sea, and that seldom and in small numbers (Kramp, 1913). In later years, however, it was found to be characteristic of the southern and central North Sea, the Skagerrak and the Scottish east coast (Savage, 1926 and 1937; Hjort and Ruud, 1929; Ogilvie, 1934; Künné, 1937). On this evidence Einarsson (1945) suggested that it had colonized these parts of the North Sea presumably during the first 20 years of the present century. Einarsson set the northernmost limit of this species in the Atlantic at the latitude of Northern Ireland. Marshall, who found it in the Orkney-Shetland region in the summer months, thought the origin of this stock to be "rather obscure," and suggested that perhaps *Nyctiphanes* had increased its area

of distribution northwards off the west coast of the British Isles as Einarsson had postulated for the east coast (Marshall, 1948).

Text-figs. 2 and 8 provide evidence in support of Marshall's suggestion. *Nyctiphanes* is now seen to extend everywhere around the British Isles and even as far north as the Faeroes, with two records of its presence off the Icelandic coast. The plot of density in Text-fig. 2 shows that the limit of its distribution in 1948 was coincident with the 100-fathom contour, and that the greatest concentrations lay to the west of Scotland, with slightly smaller numbers around the northern coast, and a falling gradient of density from the north-west to the southern North



TEXT-FIG. 5.—Graphs showing the average numbers, by day and by night, of *Nyctiphanes*, from November 1947 to December 1948, taken from the Atlantic above the Continental Shelf and in the north-western North Sea. The Shelf is defined as the water to the east of the 500-fathom contour; the north-western North Sea by the latitude of 55° North and the meridian of 3° West. The vertical scale gives numbers of euphausiids per 10 m<sup>3</sup> of water sampled. An asterisk indicate that no information is available.

Sea with a subsidiary centre in the Skagerrak. The south-eastern North Sea appeared to be almost barren. This density gradient is almost the reverse of that expected from the material available when Einarsson (1945) published his work, and it is particularly interesting that it is exhibited in the most marked form by the furcilia stages.

Text-fig. 5, showing the numbers per 10<sup>3</sup> of water, illustrates even more forcibly the paucity of the North Sea population compared with that of the Atlantic Continental Shelf. The effect of diurnal migration is also seen in its most acute form; many more adults and cyrtopia were taken at 10 metres during night than during day. Using the graphs of the night data it will be seen that the maximum densities of furcilia and cyrtopia in the Atlantic were in May and of



adults in June, whilst no increase in the numbers in the North Sea was noticed until one or two months later, in July and August, when cyrtopia and adults began to increase respectively. (The only furcilia in the North Sea occurred in August and September and were taken in the day-time.)

Mielck and Künne (1935) first suggested *Nyctiphanes* as an indicator of oceanic water entering the North Sea from the north-west. This was opposed by Einarsson (1945), who believed that it has probably established itself as a permanent inhabitant of the waters adjoining the south-flowing oceanic current in the North Sea. Marshall (1948), on the other hand, thought that together with *Themisto gracilipes* it might be used as an indicator of northern water, but he advised caution because, as he put it, of "the possibility of a double origin." His *Nyctiphanes* from the North Sea showed a wide association between adults and young, but most of his "larvae" were advanced cyrtopia stages. Künne (1937) found that both these organisms had a centre of abundance in the Flamborough-Dogger region, and he regarded this as evidence of recruitment from the north.

The post-war Recorder material from the Atlantic offers some solution to these problems. The spatial succession in 1948 is shown in Text-fig. 6, and as the material agrees with that from other years it is reasonable to suppose that this is a typical picture.

In January and February adults were widely scattered in the northern and possibly the central North Sea, but from March to June *Nyctiphanes* was absent with the exception of a few adults in the north-west and two lone captures off the Humber and the Skagerrak. In April furcilia appeared on the "W" and "X" lines over the Continental Shelf. In May and June much denser concentrations of furcilia appeared on these records, and of cyrtopia and adults on the "X" and "V" lines. There appeared to be an age gradient from furcilia in the south to cyrtopia and adults in the north (Text-fig. 6, May and June). In July the furcilia on the Shelf declined considerably, but adults and cyrtopia with a few furcilia appeared in the north-western North Sea, and in the Skagerrak.

The important point is that there was a lapse of some 2-3 months between the first increase in the Atlantic, consisting of furcilia, and the first increase off the north-east coast of Scotland ("A" record), represented by adults and cyrtopia. In the months following July the dense concentrations of furcilia over the Continental Shelf recurred, and the southerly spread of adults in the North Sea continued with diminishing numbers of furcilia until by November *Nyctiphanes* was present in the Southern Bight. The southwards movement in the North Sea appeared to take place more quickly in 1948 than in most years; Text-fig. 7 shows the succession in the two previous years. Cyrtopia and furcilia were not separately identified in 1946, but the 1947 material in Text-fig. 7 illustrates the progressive increase in age of the population with southward movement, suggesting development from a northern origin. The time interval in 1948 of three months between furcilia in the Atlantic and adults in the North Sea is about the expected interval before the appearance of O-group adults. A similar interval was observed in 1947

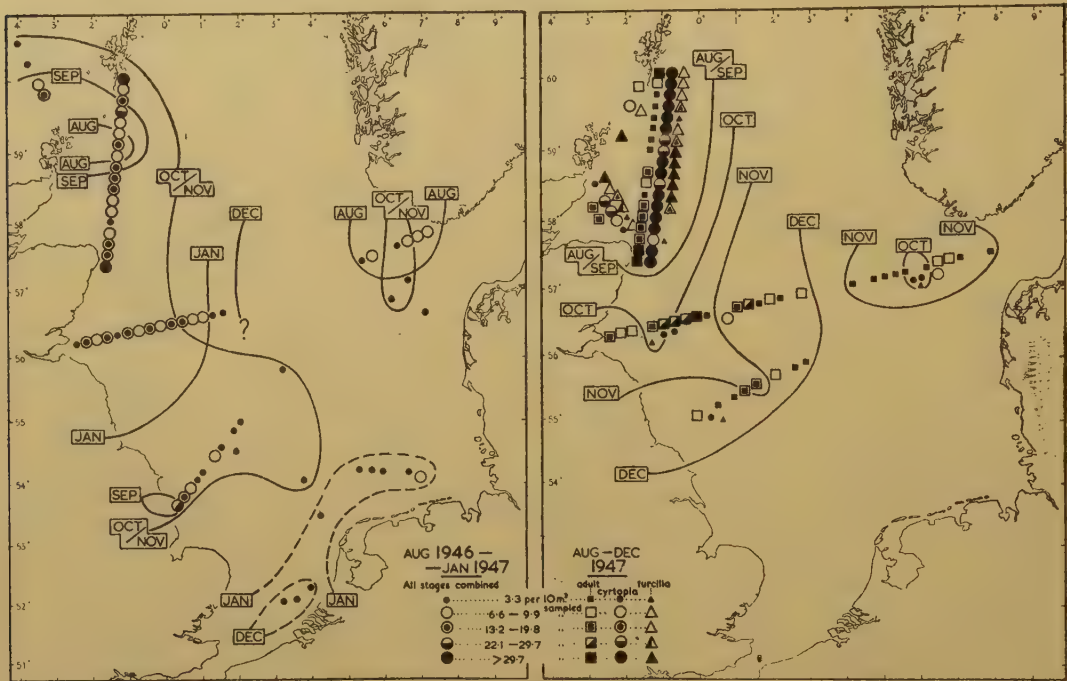




TEXT-FIG. 6.—Charts showing the distribution of *Nyctiphanes* from April to November, 1948. The months are grouped to illustrate the phases of the cycle of distribution. Sampling during night-time is indicated by a thick line, during the day by a thin line; some displacement of the records has been necessary, this is indicated by arrows at the ends of the displaced records. Adults and cyrtopia are shown above the record on which they were captured, furcilia are shown below. On the 'A' record adults and cyrtopia are shown to the left and furcilia to the right of each record. The broken line indicates the approximate limits of distribution in the North Sea (see text p. 200).

between the maximum density of furcilia in the Orkney-Shetland region in August and September, the appearance of cyrtopia off the Aberdeenshire coast in September and October, and of adults in the central North Sea in November and December.

It seems probable, therefore, that spawning off the Atlantic coasts of Scotland and Eire commencing in April gave rise to a generation of young *Nyctiphanes* which were carried northwards and then eastwards round the Scottish coasts and,



TEXT-FIG. 7.—Charts showing the southward movement of *Nyctiphanes* in the North Sea during the autumn and winter of 1946 and 1947. The unbroken lines indicate the approximate southerly limits of distribution, month by month; the symbols show the highest number found in each position during the period of the illustration. The broken lines indicate the northern and eastern limits in the Southern and Heligoland Bights in December, 1946 and January, 1947 (see text p.199). For details of the available records during the period of the illustration see Rae (1951, Plates X, XI and XII).

as cyrtopia and adults, into the North Sea in August and subsequently southwards into the Southern Bight.<sup>1</sup>

There remain two questions. Is there a spawning centre in the North Sea which might contribute to this apparent movement? Does the Skagerrak population arise from the same source as that in the western North Sea?

In 1938, 1946 and 1948 the Recorder material revealed a few *Nyctiphanes* in the Flamborough-Dogger area in advance of the expected arrival of this species from the north, as judged from the north-western records. Text-fig. 7 illustrates

<sup>1</sup> Frost (1932) has described spawning off the southern coasts of Eire in April and May.



the movement of *Nyctiphanes* in 1946 when a small, isolated patch, mostly cyrtopia, appeared off the Humber in September, apparently about one month before the northern stock was expected here. In July, 1948, furcilia and cyrtopia (3.3 per 10 m<sup>3</sup> of water) were found in the same region when the northern stock appeared to have penetrated no further than the north-east coast of Scotland (fig. 6). In neither case nor in the example from Marshall's material which follows was there any sign of breeding in the area, and in both 1946 and 1948 these isolated populations were of very short duration; there was no evidence of dispersal from the area.

In July, 1938, a similar isolated patch of adults and cyrtopia in Marshall's material was apparently two months in advance of the northern invasion. In that year the spread of *Nyctiphanes* adults and cyrtopia occurred very rapidly between September and October and involved the whole central and south-western North Sea. Marshall (1948) showed that it was unlikely that this arose from North Sea spawning, but was more probably the result of the transport of *Nyctiphanes* together with *Themisto gracilipes* and *Sagitta elegans* in a deep saline current. Subsequent vertical water mixing could have explained the apparently rapid spread of *Nyctiphanes* and *Themisto* at the Recorder depth and simultaneous mixing of *S. elegans* and *S. setosa*. Both Furnestin (1938) and Fraser (1939) have described deep water carrying *S. elegans* underneath setosa water.

Although these arguments favour water movement as an explanation of the changing distribution of *Nyctiphanes*, they do not entirely rule out the possibility that some part of its spread at 10 metres may have been caused (particularly in 1938) by the vertical migration of a residual deep summer stock or by vertical water mixing. There is, however, little evidence that this species spawns in the North Sea; Marshall's "larvae" were mostly advanced cyrtopia, and the scarcity of furcilia in the post-war material has been mentioned (p. 196). Until evidence of such spawning is produced it must be held that the major part of the winter increase derives from north-western, and as the present records show, Atlantic sources.

The distribution of *Nyctiphanes* in December, 1946, and January, 1947, is interesting (Text-fig. 7). The "C" record in December was unfortunately a short one which only sampled the eastern half of the normal route, but from the "B" and "R" records *Nyctiphanes* appears to have been absent from the Southern North Sea in December, except for a scanty patch of cyrtopia off the Dutch coast. In January, however, adults were present both in the Southern and Heligoland Bights; the broken lines in Text-fig. 7 indicate a possible explanation, namely recruitment from the Channel. Concurrently with this apparent movement from the south, the northern population appears to have retreated to the Firth of Forth area. It is tempting to surmise that this reflects a "from-Channel" flow into the southern North Sea and the retreat of the mixed oceanic and coastal waters in the north. Kramp (1913) and Künne (1937) suggested that *Nyctiphanes* may enter the North Sea from the Channel, although Künne also believed that the northern



source was important. Carruthers (1935), from continuous current-meter observations concluded that the flow of water from the English Channel into the North Sea was strongest in November with January a close second. This makes it even more significant that Kramp (1913) showed that November and February were the only months in which *Nyctiphanes* entered the North Sea from the Channel, and that December-January is the period which the present material suggests.

A further potential source of North Sea *Nyctiphanes* lies in the Skagerrak where, in all three years of the present work, a population has appeared contemporarily with the arrival of adults in the north-west. With the exception of the patch in July, 1948 (Text-fig. 6), furcilia have been very rare in the Skagerrak, both in Marshall's and the present material. Einarsson (1945) records 5 net hauls in the deep Norwegian coastal waters in August, 1931, which revealed no trace of *Nyctiphanes*, and 4 hauls in or near the Skagerrak in March, 1938, when adults only were found, presumably bearing egg-sacs, as Einarsson reports that spawning was just beginning.<sup>1</sup> However, with the exception of one individual with spermatophores and one with an egg-sac there has been no certain evidence of spawning in the Skagerrak during five years of Recorder sampling. It seems likely, therefore, that whilst some spawning may occur, the Skagerrak is not a major spawning area of *Nyctiphanes*.

Transport in deep water may help to account for the coincidence between the arrival of *Nyctiphanes* in the north-west and in the Skagerrak. Rae and Rees (1947) noticed a similar phenomenon in the example of *Metridia lucens*, and Marshall (1948) of *Sagitta elegans*. The former authors suggest that such north-western forms may be carried to the mouth of the Skagerrak in deep currents and might be absent in the upper layers; they refer to Gran (1902), who used a similar explanation to account for the entry of *Euchaeta norvegica* into Norwegian coastal waters *via* the deeper components of the Atlantic current. Such a mechanism might explain the connection between the *Meganyctiphanes* of the deep Atlantic waters to the south-west of the Faeroes and those of the deep waters of the Skagerrak.

However, these speculations do not dispel the possibility that the Skagerrak population may be independent of that of the Atlantic coasts or that there may be some North Sea recruitment from the Skagerrak. For these reasons the presumed boundaries of *Nyctiphanes* in the west have not been connected with those in the east in Text-figs. 6 and 7; this implies no more than that there is little evidence of continuity between the two distributions at the Recorder level of sampling. It is unfortunate that the Skagerrak sampling of the "K" records occurred predominantly by night, and in view of the marked diurnal migrations of this species its absence from the middle parts of these records which were mostly taken in daylight must be somewhat suspect. Some confirmation of the isolation of the Skagerrak and of the barrenness of the central North Sea at the Recorder depth may be obtained from the fact that *Nyctiphanes* was absent on the many

<sup>1</sup> Spermatophores of *Nyctiphanes* were rare both in Einarsson's and the present material.

night records on the "N," "C" and "G" routes in 1948, whilst the Skagerrak population was evident even during daylight sampling, as for example in July. That it is unlikely that the *Nyctiphanes* of the north-east contribute significantly to the main North Sea stock is further suggested by the relatively short duration of the former at 10 m., particularly in 1946 and 1947 (Text-fig. 7).

To summarize these remarks on the distribution of *Nyctiphanes*, it seems likely that intensive spawning over the Atlantic Shelf produces a stream of cyrtopia and adults which are carried northwards and then eastwards into the North Sea, arriving in the north-west in July or August. Subsequently adults penetrate southwards off the east coasts of Scotland and England, reaching the Southern Bight in November or December. An apparently separate population in the Skagerrak may be recruited *via* a deep current from the Atlantic stock. There are few signs of any regular major spawning in the North Sea but some recruitment may occur from the English Channel, possibly less regularly and certainly with less influence than the northern entry.

The apparent correlation between the distribution of a species at the Recorder depth of 10 m and the available depth of water has already been referred to (p. 189). In the example of *Nyctiphanes* and *T. inermis* this takes the form of a remarkably close correspondence between the limits of distribution and the 100-fathom contour (Text-fig. 10). On three occasions during 1946 and 1947 the "V" records took an unusual course to the north and east of the Faeroes. These records (Text-fig. 8) provided an opportunity to study the water over the ridge which joins the eastern Continental Shelf, through the Faeroes to the Icelandic Shelf. Previously and subsequently the "V" records (Text-fig. 1) sampled only the deeper water to the south of this ridge, on which records, mostly over water of 500 to 1000 fathoms depth, both *Nyctiphanes* and *T. inermis* were absent west of the Continental Slope. *Thysanoessa inermis* was found on two of these exceptional records, however, and *Nyctiphanes* on the other, extending for some 200 miles or more beyond the Slope, but over relatively shallow water of less than 500 fathoms depth (Text-fig. 8). Not only does this provide further evidence of correspondence between available depth and distribution, but it is worthy of speculation, in the light of the previous history of the northerly spread of *Nyctiphanes* (p. 194), to wonder whether it will soon reach the Icelandic Shelf and colonize the waters there. Text-fig. 8 shows the two most northerly occurrences of this species to the south of Iceland.

The consideration of *T. inermis* presents some difficulties, since furcilia of this species were not separated from those of *T. longicaudata*. In view of the distribution of adults, however (Text-fig. 3), it is unlikely that furcilia of the latter ever occurred in the North Sea.

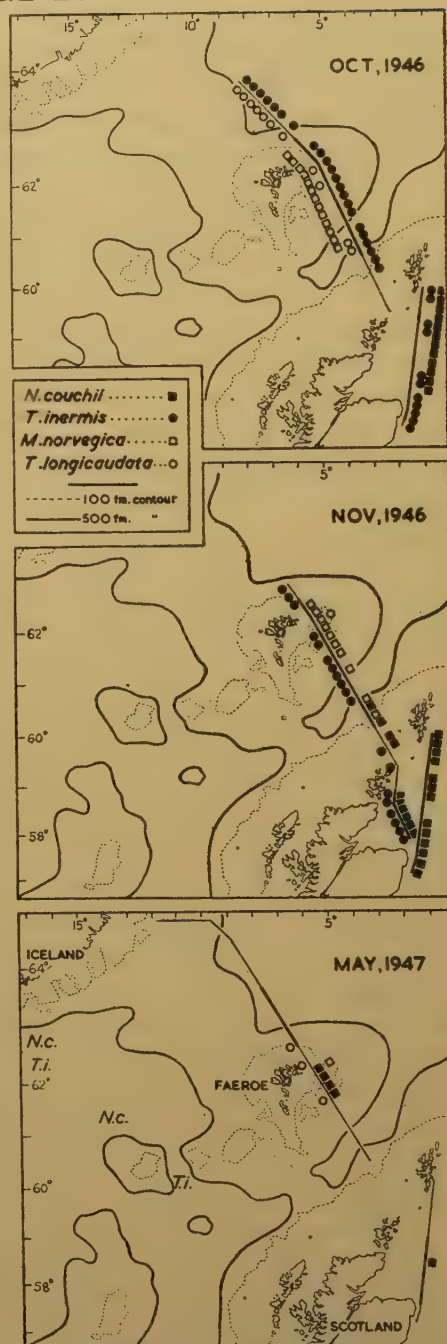
Except that it was very scarce south of a line from the Northumberland coast to Hanstholm, the distribution of *T. inermis* was very similar to that of *Nyctiphanes*. Text-fig. 3 shows that the highest number of adults occurred in the north-western North Sea; with the exception that the Skagerrak population was relatively slight in 1948, the distribution of *T. inermis* was very like that described



by Einarsson (1945) and Marshall (1948). The densities of *Thysanoessa furcilia* show that, although some spawning of *T. inermis* probably occurred off the Atlantic coast (possibly confused with that of *T. longicaudata*), there were signs that North Sea spawning was far more important.

Marshall's (1948) and the present material show a spread of *T. inermis* in the spring and early summer from the Aberdeen-Shetland region, southwards and eastwards to the central North Sea and the Skagerrak. Rae and Rees (1947) found a similar spring expansion of *Metridia lucens*, and they stressed, in view of the double entry of some indicator species in spring and in autumn, that there was a danger that ideas of water movement may be confused with the seasonal behaviour of the indicator species. However, as the above authors have suggested, it is surely significant that the two invasions which have been so characteristic of Recorder material occur at approximately the times which Tait (1937, 1949b) has described as the periods of maximum inflow of Atlantic water into the North Sea.

*T. inermis*, unlike *Nyctiphanes*, showed no connection between furcilia in the Atlantic and adults in the North Sea. The first furcilia in the North Sea in 1948 were taken in April and they persisted until July, whereas in the Atlantic they appeared a month later, in May, and except for a few adults in June this species was scarce in the Atlantic. Marshall (1948) showed a few adults in the north-west in March, 1938, followed by a spread of larvae which in June were everywhere sampled inside the area Shetland-Skagerrak-Forth, and in July showed a further southerly extension into the central North Sea. In August and in the succeeding months the distribution contracted to a small patch of adults in the Aberdeen-Shetland region (Marshall's Plates XCVIII-XCIX). In the post-war material the more detailed analysis revealed

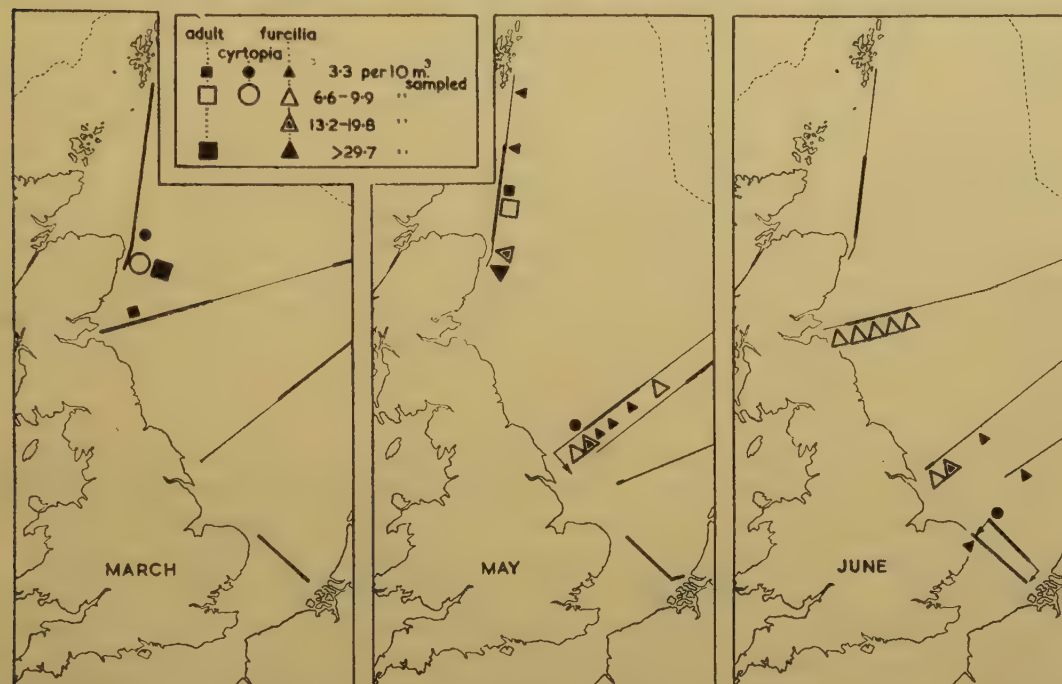


TEXT-FIG. 8.—Charts showing 3 records on the 'V' route which passed to the north of the Faeroes, with the contemporary 'A' records, illustrating the extension of the Continental Shelf species along the Faeroe-Shetland Ridge. Sampling during the night is indicated by a thick line, during the day by a thin line.



that the south-easterly expansion of "larvae" consisted entirely of furcilia stages which in 1947 extended as far as the Southern Bight (Text-fig. 9). Both *T. longicaudata* and *T. raschii* were found unusually far south in the spring of 1947 and the eastward movement of *T. inermis* towards the Skaggeirak was replaced by a south-easterly shift in that year.

There are two alternative explanations which may account for the fact that the expanding distribution of this species in the spring and summer appeared to



TEXT-FIG. 9.—Charts showing the captures of *T. inermis* in the western North Sea from March to June 1947. In February and July this species was confined to the north-western North Sea. Sampling during the night is indicated by a thick line.

There were no 'K' or 'C' records in April, which for this reason is not illustrated; adults were then present on the 'A' route.

comprise only furcilia stages. The larvae could have been transported in moving water from a localised spawning ground in the north-western North Sea, or their spread could have resulted from a progressive wave of spawning. It is difficult to resolve these alternatives with the Recorder alone. The material from five years' sampling provides evidence that *T. inermis* was represented predominantly by furcilia stages from April to June or July. This suggests a progressive wave of spawning as the mechanism of the changing distribution since Einarsson's (1945) work on growth and age implies that the furcilia of April would probably appear as cyrtopia or adults by June or July, but it is possible that furcilia transported from spawning grounds into a less favourable environment might survive for some

considerable time but have their development into cyrtopia or adults delayed. On the other hand, the absence of adults may not be significant; for a period after spawning there would be many more young stages than adults and the ratio might well be such that, when the density of population is low, furcilia would be caught by sampling 3 m<sup>3</sup> of water whilst adults would rarely, if ever, appear. An alternative explanation might be that the adults live and breed below the 10-metre level sampled by the Recorder; indeed in the pre-war material and in 1946 and 1948 the distribution lay over waters with a depth of over 40 fathoms and in such regions adults might have been near the bottom and therefore missed by the Recorder, whilst the young stages which rose to the surface were caught. In 1947, however, furcilia stages were found, although in smaller numbers than in most years, in the shallow waters of the south-western North Sea where the Recorder might be expected to take some adults even if they were near the bottom.

A progressive wave of spawning which gives the appearance of transport could be caused by a stimulus, such as a temperature threshold, being carried by water movement or occurring as a result of some climatic change. Manteufel (1938, reported by Einarsson, (1945), stated that the onset of spawning, in the western part of the Barents Sea in April and in the east in May, is coincident with the beginning of biological spring. But this west-east movement is also the direction of the main current system of the Barents Sea. Orton (1920) rejected food and, less certainly, salinity as factors controlling spawning, and suggested that sea temperature must be the most important factor controlling breeding in marine animals. Temperature being so closely bound up with wind and water movements, and these with climatic changes, it is difficult to separate the possible factors from each other. All the places in which spawning of *T. inermis* is known to occur are in various degrees affected by the Atlantic current, as Einarsson commented in the example of *T. longicaudata*. Further, the apparent movement of spawning activity in the North Sea is from north to south, which is the acknowledged direction of the water currents along the east coast of Great Britain. Therefore, whilst it seems unlikely that an Atlantic stock of *T. inermis* contributed to the North Sea population, it is probable that the southerly extension of this species in the North Sea was symptomatic of the movement of mixed oceanic and coastal water.

It is interesting to speculate on the influence of the Atlantic current on spawning activity by observing the spawning times of *T. inermis* on or about lat. 65° North described by Einarsson (1945). Norwegian waters in this parallel, which are presumably in the direct path of warm Atlantic water, are characterized by spawning in March and April; spawning is in April and May off south and western Iceland, which is probably less directly affected by the Atlantic current, and later, in May and June, off north and eastern Iceland, which is even less influenced by Atlantic water. The west coast of Greenland, which is shown by Hermann and Thomsen (1946) as receiving some Atlantic water, exhibits spawning in May and June, whilst off the eastern coast, which mostly receives cold out-flowing Arctic water, spawning is the latest of all, in July.



The material adds little to the existing information about the remaining shallow water species, *T. raschii*, which was found in all three years in the North Sea; one specimen north of the Hebrides in November, 1947, was the only adult record from the Atlantic. There is no evidence of any significant Atlantic Shelf stock and the material presents a picture of a number of isolated coastal populations lying in or near large sea inlets such as the Firth of Forth, the Moray Firth and the Skagerrak (Text-fig. 2). This agrees well with Macdonald (1928), who reported *T. raschii* in Loch Fyne on the West coast of Scotland, where spawning occurred in early spring and again in autumn; Einarsson (1945) has commented on the preference of this species for sheltered fjord localities.

Whilst small numbers of young and adult stages of *T. raschii* occurred fairly regularly in the Moray Firth and the Firth of Forth, the densest concentrations were found in the Skagerrak, where Marshall (1948) found large numbers of larvae in June and July of 1938, and particularly 1939; the present material shows furcilia and cyrtopia in May and September, 1946, and in dense concentrations in June and July, 1947. In 1948 the numbers were very low indeed and in particular very few furcilia were found (Text-fig. 2).

#### DISCUSSION.

##### *The use of euphausiids as indicator species.*

Rae and Rees (1947) and Marshall (1948) have described significant similarities in the north to south movement of different zooplankton organisms in the North Sea in 1938 and 1939; they discussed the use of these various animals as indicators of oceanic and mixed waters. A similar shift of the small cells of *Rhizosolenia styliformis* was noted by Lucas and Stubbings (1948), whilst the parallel between the distribution of some of the *Ceratium* spp. and of mixed or "elegans" water and coastal or "setosa" water was discussed by Lucas (1942). Rae (1950) drew attention to the close agreement between the movement of these indicator organisms and the date and location of spawning of herrings in the North Sea. The euphausiid material from 14 months of Atlantic sampling provides further evidence about the connection between oceanic waters and the North Sea.

So far as they go the results suggest two types of Atlantic influence on the North Sea. The first of these appears to be a regular phenomenon which may be expected in most years and concerns the shallow shelf waters of the Atlantic. This is Fraser's (1939) North Sea type II, "the mixture of coastal and oceanic water containing rich plankton with *Sagitta elegans*." *Nyctiphanes* in the autumn and winter and *T. inermis* in the spring characterize this water.

The second source of Atlantic organisms lies in the deep oceanic water beyond the Continental Shelf. This provides a less regular invasion, which occurs mainly in the autumn and winter so far as the euphausiids are concerned. *Meganyctiphanes*, which only occasionally appeared at a depth of 10 metres in the western



North Sea (e.g., 1938 and 1947), *T. longicaudata*, which sometimes penetrated to the Central North Sea (1947), and *N. megalops*, which has been taken off the Aberdeenshire coast (1938, 1939), are the characteristic euphausiids, and it might be expected that *E. krohnii* may occasionally be carried into the North Sea. This is Fraser's North Sea type I, "oceanic water containing a mixture of warm and cold water forms, *Sagitta maxima*, *S. hexaptera*, *S. serratodentata*, *S. arctica*, etc.," and to these one might add the salps and doliolids (Fraser, 1949b). There is no euphausiid characteristic of the "pure North Sea water with *S. setosa*" which is the type III of Fraser (1939) and the "setosa" water of Russell (1939).

The evidence from planktonic indicators and from hydrography as to the degree of oceanic penetration into the North Sea is not always in agreement. For example, whilst *T. longicaudata* in March and *T. inermis* and *T. raschii* in July were both found unusually far south in 1947, this year was characterized by Tait (1949a) as one in which the spring influx of oceanic water was negligible. Tait (1949b) found, however, that the autumnal influx in 1948 was much stronger than the spring one; this is certainly in agreement with the negligible penetration of *T. inermis* in the spring of that year and the complete and very rapid autumn invasion of *Nyctiphanes*. Again, Tait (1949a) from hydrographical evidence and Fraser (1949a) from the plankton, described 1947 as a year of weak oceanic inflow; this is in agreement with the relatively limited penetration of *Nyctiphanes* in that year compared with 1946 and 1948 (Text-figs. 6 and 7).

It is to be expected that the hydrographic and biological results may differ to some extent; so many factors such as the available stock, food requirements, environmental tolerance, predators and the nature of the mixing of oceanic and North Sea water must determine the extent to which indicator species lag behind or even advance ahead of the water boundaries as measured by salinities, temperatures and rates of travel of drift-bottles.

Bigelow (1926) emphasized the importance as indicators of water movement of those animals which are incapable of breeding in the area into which they are carried. In this respect the oceanic euphausiids, *N. megalops*, *E. krohnii* and *T. longicaudata*, are likely to prove valuable indicators. On the other hand, they are never likely to occur in large numbers in the North Sea, and might easily be missed by discontinuous plankton cruises; further, a 10-mile Recorder block samples only 3 m<sup>3</sup> of water and numbers are likely to be low. Russell (1936) stressed that indicator organisms should be readily identifiable, a description which fits the adults of all the three species mentioned above.

From the point of view of estimating water movement it does not matter whether animals are carried in the current, or some characteristic of the moving water changes the habit of animals previously present. For instance, if it should be shown that *Nyctiphanes* is present in the North Sea throughout the year but below the depth of Recorder sampling, it might still be used as an indicator species if changing water conditions caused it to rise to the upper 10 metres. Or again, it is immaterial to the study of hydrography whether *T. inermis* spawns only in

the north-west and the furcilia are dispersed by oceanic water, or spawns everywhere but is only under the stimulus of oceanic water. The important aim, as Russell (1936) pointed out, is to establish, over a number of years, the consistency of the behaviour of indicator organisms. The possibility that *Nyctiphanes* or *T. inermis* or any other organism may be to some extent indigenous in the North Sea does not, therefore, necessarily prevent their use as indicator organisms, providing that they repeat a pattern year after year which can be related to water movements and to the behaviour of other indicator species. But the opportunity to apply the term "indicator" to such organisms is largely dependent on a knowledge of their life histories and habits.

To that extent both *Nyctiphanes* and *T. inermis* can at present only be regarded with caution as indicators of mixed oceanic and coastal water. Both, particularly the former, have repeated a pattern for some years, and this pattern is similar to that of the other zooplankton indicator species. But it is difficult to make the best use of these species as indicator organisms until more is known in particular about the relation between oceanic influence and such spawning as may occur within the North Sea.

#### *Winter shift of Atlantic Nyctiphanes.*

Text-fig. 10 illustrates that *Nyctiphanes* in the Atlantic was confined to the shallow water inside the 100-fathom contour between January and October. In November and December of both 1947 and 1948, however, adults were found for some 60 miles beyond the contour on the "W" and "X" routes.

*Nyctiphanes* shows the most marked effects of diurnal migration, and this makes it necessary to be cautious about the validity of this winter extension into oceanic waters. At first sight there appears to be some correlation with the incidence of night and day; in order to eliminate this effect the night records only are analysed in Table II which provides a comparison between the catches of *Nyctiphanes* in its normal habitat to the east of the 100-fathom contour, and those in the 60 miles immediately to the west of the contour, the approximate limit of the winter oceanic extension.

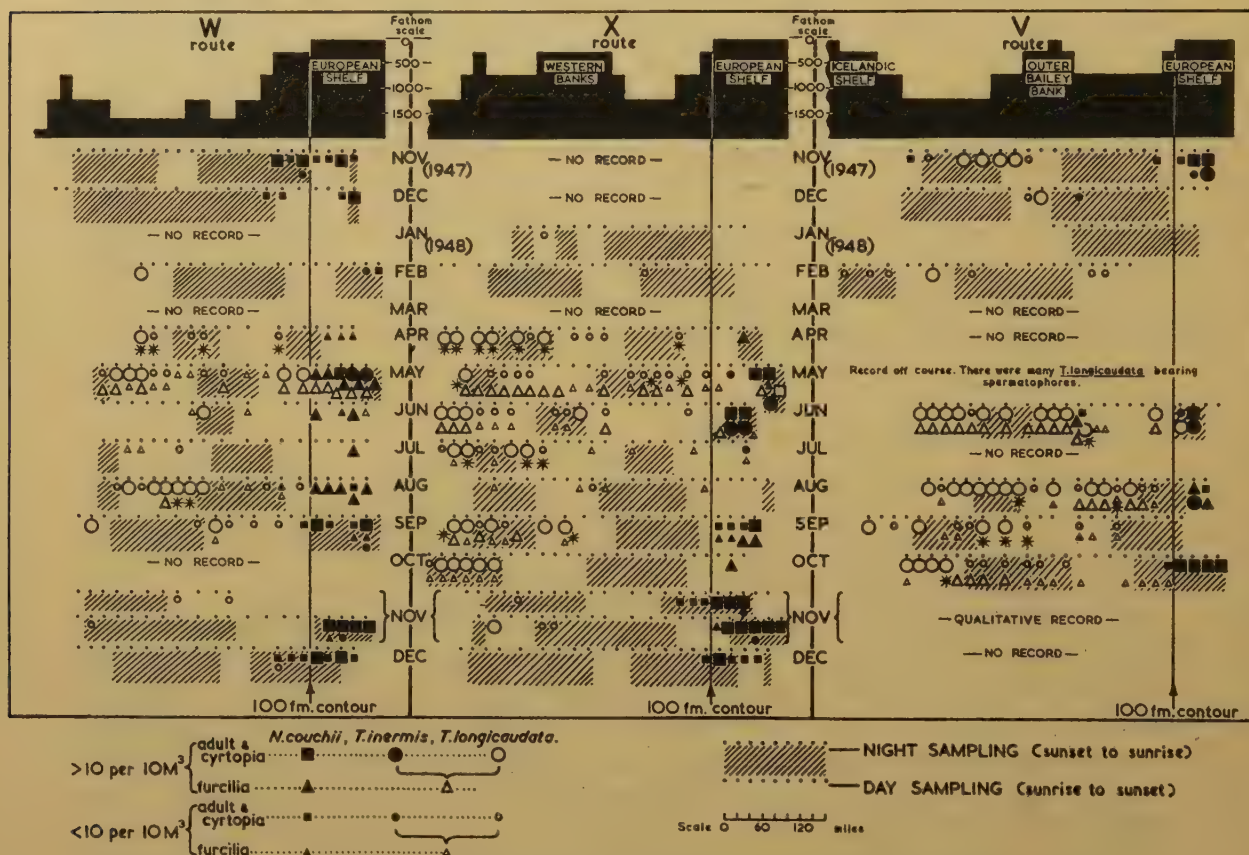
TABLE II.—*Catches of Nyctiphanes taken in Night Samples on the "X" and "W" Routes to the West and East of the 100-Fathom Contour of the Continental Shelf.*

|                                      | West of the 100-fathom contour. |                                                                       |   | East of the 100-fathom contour. |                                                                        |
|--------------------------------------|---------------------------------|-----------------------------------------------------------------------|---|---------------------------------|------------------------------------------------------------------------|
|                                      | Total catch.                    | Ratio, <i>Nyctiphanes</i> per sample<br>Nov. and Dec.<br>Jan. to Oct. |   | Total catch.                    | Ratio, <i>Nyctiphanes</i> per sample.<br>Nov. and Dec.<br>Jan. to Oct. |
| November and December, 1947 and 1948 | 30 <sup>13</sup>                | 19.6                                                                  | . | 162 <sup>21</sup>               | 1.2                                                                    |
| January to October, 1948             | 2 <sup>17</sup>                 |                                                                       | . | 133 <sup>21</sup>               |                                                                        |

The indices show the number of night samples analysed.



Although the material is insufficient to give a decisive test of the hypothesis it suggests that the population density to the west of the contour was nearly 20 times greater in November and December than during the rest of the year, and that this was not accountable to seasonal changes in the abundance of *Nyctiphanes* or to the incidence of night sampling. Further strength is added by the observation that during the



TEXT-FIGS. 10 and 11.—Diagrammatic sections of the sea-floor on the Atlantic routes showing the euphausiids collected, from November 1947 to December 1948. The incidence of night and day is also shown.

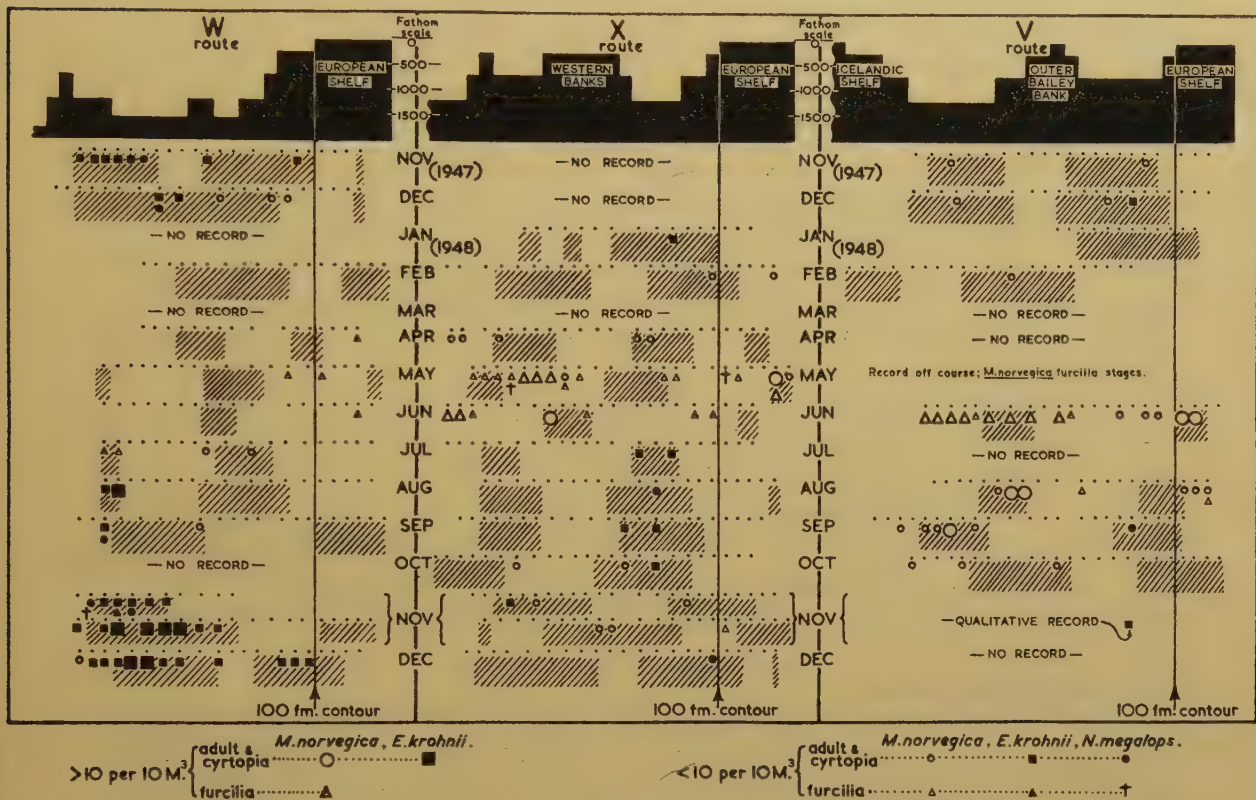
Each dot represents a ten-mile Recorder block; irregularities in the spacing of the dots arise from the ships' deviations from course, each block is positioned by the depth of water over which it was taken.

Asterisks indicate the presence of *T. longicaudata* bearing spermatophores.

summer months when adults and furcilia were numerous during daytime on the "W" and "X" records, they did not extend beyond the 100-fathom contour. A brief examination of the Recorder blocks near the contour in the winter of 1949-50 shows a similar slight extension of *Nyctiphanes* in November, 1949, when the incidence of night and day could not have been responsible, and in February, 1950, when *Nyctiphanes* did coincide with night sampling.



Cooper and Vaux (1949) showed that as a result of surface cooling in the winter, water may flow from the Continental Shelf and "cascade" down the slope into considerable depths of the ocean. They advanced the theory that cascading would result in the plankton of the shallow Shelf being carried down into deep water off the Slope. Presumably the weaker swimmers would be unable to free



TEXT-FIG. 11.—(See opposite).

themselves from the descending cascade, whilst the large powerful swimmers would extract themselves at some depth outside the Shelf which was not beyond the range of their diurnal migrations. This segregation of plankton would show itself by a collection, beyond the slope, of large vigorous zooplankton forms whose normal habitat lay over the shallow shelf waters. It should, therefore, be possible as Cooper and Vaux said, to name indicator organisms by which cascade water may be identified. The cascading described by these authors occurred in the Celtic Sea to the south of Ireland. They examined the possible sources for replacement of water removed by cascading, and favoured a compensation current of Atlantic or Biscayan surface water flowing in an easterly direction as the Shelf waters sank and cascaded in a westerly direction.

To judge from their marked vertical migrations euphausiids are capable of vigorous swimming, and might be expected to show the effect which Cooper and Vaux postulated. Whilst the present material must be treated with considerable caution it may be that *Nyctiphanes* appeared, in its winter oceanic extension, to show the direct effect of cascading, namely the transport of shelf species to a more oceanic habitat. Fig. 11 ("W" route) shows that *E. krohnii* apparently moved in the reverse direction, from oceanic to Slope waters during October-December. Unfortunately the incidence of night and day sampling is such that this movement is suspect, but it is possible that it represents the movement of surface replacement water from the west.

More material will be required to test this hypothesis which is mentioned here to provide a possible example of a planktonic indication of the type which Cooper and Vaux postulated. Even if further proof should be available there may be alternative explanations. For instance a slackening of the speed of the Atlantic current in winter could result in greater mixing between oceanic and coastal waters with a corresponding shift of Shelf plankton westwards and of oceanic plankton eastwards.

Nansen (1913), reported by Cooper and Vaux, has described cascading from the Rockall Bank, but the present material gives no indication of this; most of our records lay to the north of Rockall itself. The water over the Western Banks was usually rather bare of euphausiids compared with that on either side (Text-figs. 10 and 11, route "X"), but this was an all-the-year-round phenomenon and may be the result of the current system (see p. 190); certainly cascading is unlikely to account for such a scarcity of euphausiids over the Bank in summer.

#### *Vertical migration.*

Marshall (1948) drew attention to the danger which besets the interpretation of the Recorder collection of euphausiids and which arises from the marked diurnal migration of these animals. He showed that the incidence of all the species was greater during night sampling than by day. The present material shows the same effect which is generally most marked in the example of the adults, less so in the cyrtopia, and is negligible or even reversed in the example of the furcilia. One exception is *T. longicaudata*, of which more of all stages were taken by day than by night (see p. 192).

It is difficult to measure the effect of this bias since it is probable that there are seasonal variations in the extent of diurnal migrations, and it is not easy to separate the effects of differences in geographical distribution from those of vertical migration. The seasonal appearance in the Recorder material of euphausiids such as *Euphausia krohnii* and *Nematoscelis megalops*, for instance, may be an artifact arising from the seasonal ratios of night to day. On the other hand, as Russell (1936) remarked, there is evidence that many plankton animals seek deeper layers in winter; all the euphausiids show a minimum, usually in January and February, which might be the result of this tendency.



For these reasons no attempt has been made to estimate the extent of the bias caused by the effects of diurnal migration. In describing and discussing the distribution of the euphausiids allowance has been made for its possible effects; it has been necessary to consider at every stage the effect of using only night or only day-time collections. The incidence of night and day is illustrated in Text-figs. 6, 8, 9, 10 and 11. In particular the evidence for cascading (p. 207) must be considered tentative in view of this feature of Recorder collections; material from a number of years would be needed to provide a thorough test of its validity.

#### A PARASITE.

Einarsson (1945) found large numbers of *T. inermis* in Icelandic waters to be infected with a parasite, an ellobiopsid, which he regarded as probably of the genus *Amallocystis*. He also noticed it on specimens of *T. raschii* from Faxaflói, to the west of Iceland.

A similar parasite was found on *T. raschii*, on two successive records in the region of May Island in the Firth of Forth, on July 30th and August 27th, 1948. On each occasion the infected specimens were adults and the parasite was attached, as were Einarsson's examples, to the dorsal side of the carapace. The incidence was two infected in a total of nine adults, and it is interesting that with such a small sample, these, the only parasites in the Recorder material, should have occurred on two successive records and in the same place.

Boschma (1949) in his monograph on the Ellobiopsidae in the Discovery Collection, gives a description of the external characters of these parasites. Those in the present collections accord completely, so far as external characters are concerned, with Boschma's description of *Amallocystis fagei* Boschma. All previous records of this species refer to the Antarctic; Boschma (pp. 288, 289) believes, however, that the specimens of *Staphylocystis racemosus* recorded by Macdonald (1927) on *Meganyctiphanes* in the Clyde Sea and of *Amallocystis* spp. recorded by Einarsson (1945) were in reality *A. fagei*. It therefore appears unlikely that the appearance of this parasite in northern waters is a recent phenomenon although Macdonald's reference (1927) was the first to be published.

#### SUMMARY.

1. The distribution of euphausiids collected in the North Sea by the Continuous Plankton Recorder during 1946, 1947 and 1948 and in the eastern North Atlantic during 1948 is described.

2. These euphausiids fall into three groups, each characterised by the depth of water above which they were captured. These groups comprise:

- i. Oceanic species found over deep water (*Euphausia krohnii* and *Nematoscelis megalops*).
- ii. Oceanic species found over a wide range of depths (*Meganyctiphanes norvegica* and *Thysanoessa longicaudata*).



iii. Shallow water species (*Thysanoessa raschii*, *T. inermis* and *Nyctiphanes couchii*).

3. The members of the first two groups appear irregularly and in small numbers in the North Sea, where their distributions correspond with Fraser's (1939) oceanic water containing a mixture of warm- and cold-water forms.

4. The third group consists of regular inhabitants of the North Sea. *T. raschii* is mainly found in the Skagerrak and there is probably no recruitment from the Atlantic. The distribution of *N. couchii* and *T. inermis* and their movement in the North Sea correspond closely with those found by Rae and Rees (1947) for copepod indicator species of mixed water, by Marshall (1948) for other zooplankton, with the "elegans" water of Russell (1939) and with Fraser's (1939) mixed coastal and oceanic water.

5. The main origin of *Nyctiphanes* in the North Sea and the major spawning area are shown to lie in the Atlantic, over the Continental Slope.

6. A slight extension of *Nyctiphanes* over deep water in the Atlantic in winter is tentatively related to the phenomenon of "cascading" water described by Cooper and Vaux (1949).

7. *Amallocystis fagei*, an ellobiopsid parasite, has been found on *T. raschii* in the North Sea.

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# CONTINUOUS PLANKTON RECORDS: THE YOUNG FISH AND FISH EGGS, 1932-39 AND 1946-49.

BY

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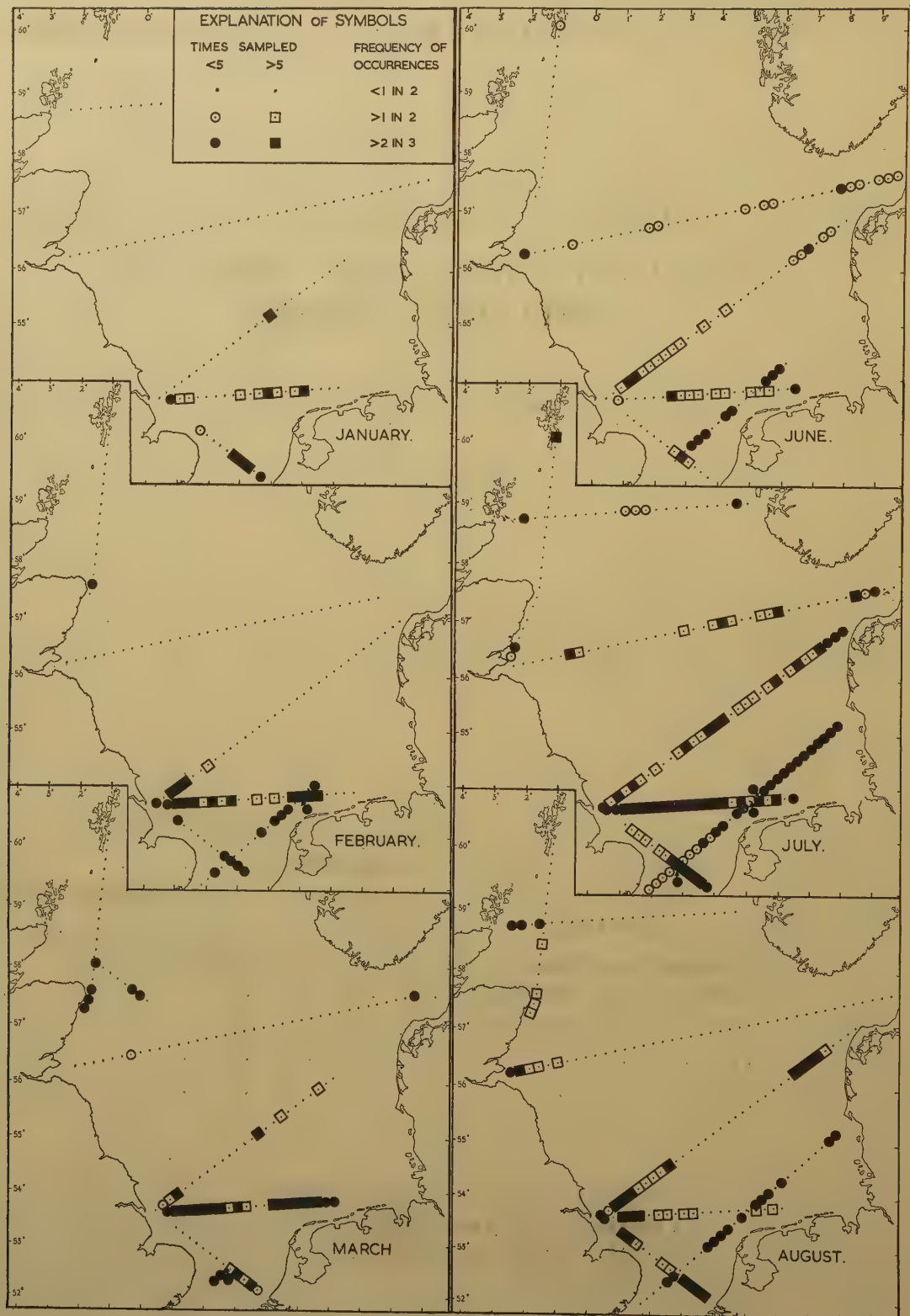
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## INTRODUCTION

THE material on which this paper is based was collected in the course of the Continuous Plankton Recorder survey of the North Sea and adjacent waters during the years 1932-39 and 1946-49; the method and scope of the investigations have already been described (Hardy, 1939, 1941; and Rae, 1952). Up to 1937 the survey was limited to the southern North Sea, but in 1938 it was enlarged to cover

III, 24. 1





TEXT-FIG. 1.—Selected monthly charts of the frequency of occurrence of young fish on each 10-mile block on the routes in the North Sea. A circle denotes that a particular block has been sampled between three and five times during the survey, whereas a square denotes that it has been sampled between six and fifteen times.

the greater part of the area northwards to a line from the Shetlands to Norway. In the spring of 1939 a route in the Atlantic, extending from the Pentland Firth towards Iceland, was added. From 1946 onwards most of the pre-war routes, or very similar ones, have been resumed, and there has been a considerable extension of sampling in the Atlantic.

The outbreak of war in 1939 brought the survey temporarily to a close, although for a time laboratory studies were continued. Dr. Stubbings was thus able to complete a re-examination of the young fish collected up to 1939, and he drafted a preliminary account of the results, and prepared figures illustrating them. These figures have now been published separately (Stubbings, 1951) with an abridged explanation.

The author is greatly indebted to Dr. Stubbings for the very extensive tables and distribution charts which were prepared from the pre-war material, and for the preliminary results of the many lines of investigation which were initiated, all of which have been of material assistance in the preparation of this account. Many of the suggestions embodied in the original draft have been developed here.

It should be understood that in view of the relatively small numbers of specimens involved (see p. 218) the policy has necessarily been one of summation and average, as often the detail is of insufficient significance to stand by itself. Yet it must equally be emphasized that even the smallest numbers take on a greatly increased significance if they occur regularly in the same places in successive years, and so build up patterns of distribution which are repeated without major variation. The cumulative effect of such regular occurrences, without regard to the actual numbers caught on any occasion, is shown in Text-fig. 1 for some selected months, in which the frequency of occurrence of total young fish is plotted for the routes in the North Sea. The solid symbols denote the blocks<sup>1</sup> on which young fish have been caught on at least two out of every three occasions of sampling, the open ones indicating captures on at least one out of every two occasions. This repetition of occurrences is also evident in some of the individual species studied, and may be seen in Text-figs. 2, 3 and 4 for the *Clupea spp.*, *Scomber scombrus* (mackerel) and *Gadus poutassou* (the poutassou) respectively. Note, however, that these charts show the actual distributions, that is the number per sample, in the years figured, not just the frequency of occurrence.

The overall picture of the composition of the young fish and fish eggs in the plankton presents some anomalies when compared with the results which might be expected from previous knowledge of the adult stocks. Comparatively few larvae were found of some species known to be abundant, while some of the commoner species were not included among the eggs identified. This may well be due to the peculiarities of the technique; the recorder samples at a single fixed depth, 10 metres below the surface, and all the catches are obtained from fixed routes which may not traverse certain spawning areas. Nevertheless the results are comparable *inter se*.

<sup>1</sup> Approximately 4 in. × 4 in. of silk which has filtered about 3 cubic metres of water.



## METHODS AND MATERIAL

The limitations of the recorder method are fully discussed in earlier Bulletins, particularly by Hardy (1939), Lucas (1940) and Rae and Fraser (1941), but some points which apply particularly to the young fish and fish eggs require comment here. The crushing of organisms between the silks, although diminished after 1937 by improvements in the mechanism (Hardy, 1939, p.25), still occurs at times in the case of the relatively soft-bodied young fish which may be pressed so firmly into the meshes that they cannot be removed for separate examination. This crushing may result in distortion of shape, damage to or obscuring of pigment patterns, the breaking away of a long gut or the loss of a tail, or the impression of a "mesh pattern" which often prevents a reliable myotome count. Consequently a residue of individuals is left which at best can only be assigned to genera (or perhaps to a group of species within a genus) and at worst may have to be recorded as completely unidentifiable. However, by careful selection of the grouping to genera, etc., this latter category is no longer so significant, as it contains only 5% to 6% of the total specimens. It is doubtful whether this figure can be reduced much further without a disproportionate expenditure of time.

These factors also operate in respect of the fish eggs where, together with the shrinkage and opacity resulting from fixation in formalin, they limit severely the value of measurements as an aid to identification. The larger eggs, particularly of plaice, may sometimes be identified on the basis of their size and time of occurrence, but the certain identification of many of the remainder depends on the chance that there is a recognizable embryo visible within the egg. Nevertheless, it has been possible to identify a few from time to time, often from the larger concentrations, and on circumstantial evidence to infer the probable identity of many of the remainder.

Special consideration has been given to the specific identification of the young stages of the important food fishes, the remainder usually being referred to genera. In the earlier part of the survey, up to 1937, only some 8% of the collections could be given specific identity, while some 73% were referred to genera, leaving a residue of about 19% which were unidentifiable. In 1939, however, about half of the specimens of *Gadus* caught could be identified specifically even after some months of storage, while from 1946 onwards there has been a further increase in the percentage referred to species, and the residue of "unidentifiable" has fallen to about a quarter of its original level.

The standard depth of tow of 10 metres, the mesh of silk, and the size of intake currently used in the survey are not necessarily the most suitable for obtaining large numbers of fish eggs and young fish. The samples are very small, the numbers of young fish on a 10-mile block only occasionally exceeding 20, and commonly being below 10. This is not due to any limitation in the catching power of the instrument, as on occasion it has caught as many as 130 young fish (*Clupea harengus*) and the catch of fish eggs has twice exceeded 150, on a single block, or per 3 cu. m.

of water filtered. There remains the difficulty that individual species, with the exception of the Clupeidae and Ammodytidae, may be represented by very few individuals in the course of a season, and efforts are being made to increase the numbers of young fish caught by a modification to the intake aperture of the instrument. This limitation in numbers has meant that for most purposes the material can only be treated in generic groupings, with comment on the specific composition.

There have been occasional interruptions in the series of records from all the routes sampled;<sup>1</sup> but these gaps are relatively infrequent and are not considered to be serious, except in 1946, when the survey was being resumed after the war and routes could only be restarted at intervals. Consequently caution must be used when comparing the summarized results for 1946 with other years, as the sampling was very limited for the first six months.

In spite of these limitations the seasonal variations in abundance can be shown to follow substantially similar courses from year to year, and assessments of the abundance of different genera, or groups, of young fish in the several years offer some opportunities of examining the ultimate success of the year class concerned. The overall changes in abundance over the period studied are also compared with the trend shown by the results of studies at Plymouth.

#### ARRANGEMENT AND TREATMENT OF THE DATA.

In the plates already published (Stubbings, 1951) sets of charts, covering the months in which the larger numbers occur, are shown for the total fish eggs, the total young fish excluding the Clupeidae, the Clupeidae, the Ammodytidae, and the Gadidae and Pleuronectidae. Average annual distributions of the Clupeidae and Ammodytidae are also figured. This account cannot, unfortunately, be illustrated on the same scale as the earlier one,<sup>2</sup> so that summarized distributions only can be shown.

The composition of the group shown as "total young fish" has been changed so that both Clupeidae and Ammodytidae are excluded, whereas in the earlier figures only the Clupeidae were omitted. This exclusion of the bottom spawning *Clupea harengus* and the *Ammodytes* spp. allows a closer comparison between the totals of young fish and the fish eggs. The eggs of *Clupea sprattus* will therefore contribute to the total of fish eggs, although the young will not be counted among the young fish; as however *Clupea sprattus* has been found so much less commonly in our material than *Clupea harengus*, it is believed that the error so introduced can only be slight.

In the earlier years of the survey, in particular before 1937, there were some changes in the method (Hardy, 1939, pp. 36-47) which affected the size of the intake

<sup>1</sup> Due to the towing ship being off service, to bad weather preventing a tow, or to a partial or complete failure of the mechanism.

<sup>2</sup> Details, plotted or tabulated, can be made available on application to the Officer-in-Charge, Oceanographic Laboratory, 78, Craighall Road, Edinburgh, 5.



aperture on the recorder and the rate of winding of the silks. In the plotting and summation of the young fish and fish egg data all these variations have been allowed for; the figures given are related to the standard 10-mile blocks, and to the  $\frac{1}{2}$  in. sq. aperture now in use.

In summing the data for individual years, the figures, with one exception, are based on the months January to August (or September) only, as the numbers caught in the remaining months of the year are negligible. For the *Clupea spp.*, however, all twelve months are included. The figures or symbols plotted on charts showing distributions represent the actual catches per 10-mile block in Stubbings's account (1951), but it has been found convenient here to relate the figures to a standard volume sampled, based on the theoretical filtration of 3 cubic metres per 10-mile block. The mean level of sampling for the southern North Sea from 1932 onwards was 153 cubic metres per month from January to August, the figures in the autumn usually being higher due to extra sampling (Lucas, 1940, p. 74 and footnote), so the numbers are related to a standard 100 cubic metres sampled.

Several additional species have been identified in the material collected from 1946 onwards, as follows:

|                                                         |                                        |
|---------------------------------------------------------|----------------------------------------|
| <i>Scomber scombrus</i> (Linn.).                        | <i>Gadus pollachius</i> (Linn.).       |
| <i>Crystallogobius nilssonii</i><br>(v. Dub. und Kor.). | „ <i>minutus</i> (O. F. Müller).       |
| <i>Chirolophis galerita</i> (L.) Walb.                  | „ <i>luscus</i> (Linn.).               |
| <i>Drepanopsetta platessoides</i><br>(Fabr.).           | „ <i>esmarki</i> (Nilss.).             |
| <i>Solea variegata</i> (Donov.) Flem.                   | <i>Merluccius merluccius</i> (Linn.).  |
| <i>Lebetus scorpioides</i> (Collett).                   | <i>Molva molva</i> (Linn.).            |
| * <i>Fierasfer dentatus</i> (Cuv.).                     | * <i>Gadiculus argenteus</i> (Guich.). |

Those marked with an asterisk were taken only on the Atlantic routes, and some are represented by only one or two specimens. Three further individuals of *Anguilla spp.* have been collected, one of which is in the leptocephalus stage. Several species of the Scopelidae were taken on the Atlantic routes in 1948 and 1949, but the material is not yet sufficient to permit of any conclusions in respect of seasonal distribution or abundance. The following have been identified: *Myctophum glaciale* (Reinh.), *Myctophum humboldti* (Risso.), and *Maurolicus mulleri* (Gmel), but only the first of these has occurred in appreciable numbers and with any regularity.

#### DISTRIBUTION OF THE YOUNG FISH.

Stubbings (1951, Plates CXII–CXV) shows series of charts for the years 1932–1939 illustrating the distribution of all the young fish combined, excluding the Clupeidae. It is important to study these in conjunction with the series showing the Ammodytidae (*ibid.*, Plates CXVIII, CXIX, CXXI and CXXII) as the latter are dominant at times, especially in February and March, and thus obscure the distribution of the other young fish.



Over the whole period studied the areas of abundance, or frequent occurrence, of young fish (excluding the Clupeidae and Ammodytidae) are broadly similar to those determined for the fish eggs. In each year aggregations occur east of the Humber, extending over the south-west part of the Dogger Bank; off the Frisian Islands and in the Heligoland Bight; and in the Flemish Bight. The large numbers found in the central part of the North Sea in some years agree well with the corresponding egg distributions, and this agreement is maintained in the results from the routes further north. The relation between the numbers caught in the several years, and the comparison of these with the data for fish eggs and commercial catches are dealt with in a later section, where the summed figures are discussed, but it is evident from the charts (Stubbings, 1951) that the years 1938 and 1939 show the largest numbers and the most widespread distribution of the pre-war period, allowing for the wider coverage available in these two years. *Gadus spp.* and *Pleuronectes spp.* are very important contributors to the large number in these two years, and this is seen also in 1946 and 1947, when the numbers were of comparable value, but there is then a decline to a low level in 1949.

(a) *Clupeidae*.

In the earlier material the clupeids were not identified specifically, and even in the later material the separation of *Cl. harengus* (herring) from *Cl. sprattus* (sprat) was not always certain (see p. 218). Their distribution is therefore shown as that of a generic group, although it is possible to suggest the identity of most of the concentrations. The series of charts shown by Stubbings (1951, Plate CXV) for the average monthly distribution throughout the year has been extended and brought up to date and is now shown as Plates XXI and XXII, in which the details stand out clearly. It seems fairly certain that, with the exception of the English Channel and Irish Sea, all the important herring spawning areas are sampled, although only those in the North Sea are figured. Those off the north-west coast of Ireland and off the northern outlet of the Minch are sampled by the Atlantic routes, but the data is limited, so they are not included.

In that part of the North Sea lying to the south of Lat.  $55^{\circ}$  N. there is general agreement with the distribution of herring larvae from October to April as shown by Wallace (1924) and with the spawning areas given by Hodgson (1928), while further up the east coast of England the spring and autumn herring spawnings off the Northumberland coast are represented by catches of young clupeids in our records. In the area from the Firth of Forth to Shetland the spring spawnings of herring are but scantily represented in our material, even in April and May, but the summer-autumn spawnings are clearly shown by the patches on the Leith-Lerwick and Leith-Copenhagen routes, and agree generally with the centres of herring spawning given by Bowman (1922), and shown in the 'Herring Atlas' (1950). The concentrations of young clupeids in the summer and autumn show three important aspects of the results obtained from the Recorder survey, and for each of the four post-war years a sequence of five months is shown in Text-fig. 2. In the



TEXT-FIG. 2.—Charts showing the distribution of young Clupeidae in the North Sea from July to November for the years 1946–49. The 10-mile blocks are paired, so the symbols indicate the numbers per 20 miles.



area off the Humber in October of all four years the repetition of occurrences of low numbers is well demonstrated, emphasizing the regularity of this patch (see also the October chart in Plate XXII). The well-defined patches off the north-east coast of Scotland in August, September and October, which contain a high proportion of individuals of from 7 to 10 mm. in length, are also repeated with marked regularity and appear to be the direct results of spawning in this region. Examples of the large fluctuations in actual numbers within such patches which may occur from year to year can be seen by comparing 1946 and 1947 with the two following years, when the numbers are very much reduced in this area. This fall in numbers is evident also in the Southern Bight of the North Sea, where in July and August the 1947 patch is barely represented in the two following years, although its existence is supported by the results from the pre-war years (see the July and August charts in Plate XXII). The small spawning ground off Hanstholm, over the Jutland Bank area, from which the "Jutland coast autumn herring" derive (Paulsen, 1936, p. 20), does not appear to be defined in our material, but it is stated that the spawning is "quite insignificant" (Paulsen, 1931, p. 9), so the number of young may be too limited to be evident in our results, although a few are found in July and August.

The concentrations found close to the Norwegian coast in March, April and May, although based on relatively few records, are in reasonable conformity with the spawning in this area, and this is amplified by recent data from the Norwegian Weather Ship's route from Bergen on which herring larvae are found in April.

It seems reasonable, therefore, to consider the young Clupeidae of the Recorder survey, which can be related to known spawnings and spawning areas of the herring ('Herring Atlas,' 1950), as being predominantly *Clupea harengus*, accepting the possibility that there may be a small percentage of sprat included at times in the light of the long spawning period ascribed to it by Ehrenbaum (1927). This applies to all concentrations figured except those occurring in the southern part of the North Sea in June, July and August, among which *Clupea sprattus* has been identified. These concentrations are clearly separated in time from all the others found in this part of the North Sea, the months of May and September being practically blank. They are not continuous in space with the herring spawning known to be in progress during these months off N.E. Scotland. Robertson (1938) in his account of the sprat fisheries quotes many authorities on the spawning of *Clupea sprattus* and concludes that the distribution of the larvae can be stated in the same terms as that of the eggs and : "extends over the whole of the Southern Bight of the North Sea and along the German and Dutch coasts. The month of greatest abundance (*of eggs*) is June and the greatest concentrations . . . occur in the German Bight . . . also . . . off the coast of Jutland, on the Fisher Bank and in the Skaggerak . . . from the Wash and between the English and Dutch coasts." The occurrence of maximum numbers of young in July in our records agrees satisfactorily with a June egg maximum, and the correspondence between the distribution of the young Clupeidae in the southern North Sea in June, July and August and the description quoted above leaves little doubt that the young of this period are predominantly *Clupea sprattus*.



There may be some herring off the Jutland coast at this time, but they are not very abundant (see above) and in any case are well to the north of our main concentrations. It would seem unlikely that there is any significant persistence of sprats after August to mix with the herring of October onwards, as practically no larvae were found in this area during September. On the other hand, it is possible that sprat are present among the clupeids found in this area in March and April, as Simpson (1948, 1949) finds some sprat eggs and young in the Southern Bight at this time, yet May, like September, is singularly unproductive of any clupeid young. There would thus appear to be an interruption in the spawning, if it does actually begin as early as March, to account for the virtual absence of larvae in May (Plate XXI).

(b) *Ammodytidae*.

Since the beginning of the survey these have been treated as a group and no specific identifications have been attempted. In the light of the current revision of their specific characteristics (Raitt, 1934; Kandler, 1941; Corbin and Vati, 1949; and Einarsson, 1951, who quotes several other authors) there must be some doubt as to the validity of some of the identifications previously accepted. According to Einarsson (1951) it appears probable that there are three species, *A. lanceolatus*, *A. lancea*, and *Gymnammodytes semisquamatus*. Of these *A. lancea* may be found to have three sub-species, varieties or races, viz.: *A. lancea lancea*, *A. lancea marinus* and *A. lancea dubius*, although some doubts have still to be resolved on the separation of the last two.

Our records show two periods in the year in which young *Ammodytes* spp. are regularly found, of which the earlier is the more important quantitatively. The first, the "spring" period, runs from February to April, but may actually commence in the extreme south-east in January and persist into May in the north-west. The distribution tends to be coastwise initially, and to spread offshore from the coasts; it commences and terminates earliest in the south-east and latest in the north-west. There is a small concentration off the Jutland coast in April, but in June very few are recorded apart from a small patch off the Firths of Forth and Tay, which has persisted from a larger April-May concentration in this region. The second, "autumn" period of occurrence of *Ammodytidae* in our records is shorter, limited usually to July and August, but extending occasionally into September. It appears to be quite distinct, as the individuals caught were of small size, and obviously of recent hatching; there was no continuity in space between these and the small remnant of the April-May patch which persists into June off the Firth of Forth. The distribution is mainly in the south and east, but there are patches off the Jutland coast in July and August, and to the east of the Pentland Firth in August, the latter being the only important concentration in the north-west.

(c) *Pleuronectidae*.

The additional material available from the post-war years makes it possible to show average distribution charts for this group, which was shown by Stubbings.

(1951, Plates CXXIII and CXXIV) without distinction of species. The average distributions for the months January to August are shown in Plates XXV and XXVII, with additional notations indicating the species found. Only a limited number of species are thus indicated, and the presence of any particular notation depends on the occurrence of large numbers, or the frequent recurrence of small numbers, of the species concerned. This method of illustration has been selected as most of the species recorded, except for *P. platessa* (plaice) and *P. limanda* (dab) which were caught in fair numbers, are represented by very small numbers, often widely scattered.

Very few young pleuronectids are found in January, and the numbers are not much greater in February, but the occurrence of plaice larvae can be referred to the concentrations of eggs depicted by Buchanan-Wollaston (1926, charts) and the drift of these larvae followed from the Southern Bight in a north-easterly direction towards the nursery grounds of the Heligoland Bight and Jutland coast. In March appreciable numbers of dab are also found, the densest concentrations now lying north-west of Terschelling, and this agrees well with the distributions figured by Simpson (1948, 1949) although his data do not extend past the middle of the month. The participation of *Pleuronectes flesus* (flounder) in these spring concentrations is not so clearly shown, however, by our data as by his figures. In April the densest patch of young has drifted further to the north and east, and it seems probable that the diminution in May, which is noticeable, is due to the metamorphosed young having completed the planktonic stage of their development (Heincke, 1905, p. 16). In April there are some signs of a more general distribution of young pleuronectids, which is more marked in May, although the numbers remain generally low, but except for one or two isolated occurrences it is not until June that species other than plaice and dab occur in any number or with any frequency. In June, too, the density increases to some extent, this increase being more marked in July, but in August the numbers have fallen again and the occurrences are scattered. After August the numbers caught are relatively insignificant and have not been plotted. *Pleuronectes cynoglossus* is widely distributed in June and July, but the numbers are very low, while of the remaining species only *Pleuronectes microcephalus* and *Solea vulgaris* (common sole) occur (mainly in June and July) with any regularity. The isolated and occasional identifications of *Drepanopsetta platessoides*, *Rhombus maximus*, *Solea variegata*, *Solea lutea*, and *Arnoglossus laterna* depend on so few specimens that they afford little useful information.

(d) *Gadidae*.

This group was combined in the charts shown by Stubbings (1951), but it is now possible to treat it in fuller detail, and the average distributions for the months January to August are shown in Plates XXVI and XXVII where the symbols are annotated on the same basis as for the Pleuronectidae.

Although there is an indication in January of the occurrence of young *Gadus callarius* (cod) in the Southern Bight it is not until February that the numbers.



become appreciable, in which month *Gadus merlangus* (whiting) also are recorded fairly commonly, and there is a small patch of *G. virens* (saithe). The distribution in these two months is limited to the south and east, but in March there is a scattering of young further west, while the densest patch is located off Terschelling (as was found for the Pleuronectidae) and whiting and cod are by far the most important contributors. Saithe are found in small numbers further off the Heligoland Bight than the position of the dense patch of cod and whiting and they are also recorded off the Firth of Forth. A few *Gadus aeglefinus* (haddock) are recorded on the Leith- and Hull-Copenhagen routes, but the actual numbers are very small. The distribution in April, however, extends over almost the whole area sampled, whiting predominating in the records. The densest concentrations of whiting are found in and off the Heligoland Bight. May shows broadly similar conditions, but the density of young, particularly in the Heligoland Bight, is considerably reduced, and although whiting is still common, there is an increased contribution from other *Gadus* species (*G. pollachius*, *G. minutus*, *G. luscus*) with some occurrences of *Onos cimbrius* and *Molva molva*. A few haddock were found from 3°-5° E. longitude on the Leith-Copenhagen route. In June and July, the total numbers have increased to some extent, still with a large component of whiting with some haddock, east of 1° E. on the Leith-Copenhagen route, and at about 4° E. on the Hull-Copenhagen route.<sup>1</sup> Cod contributes to the numbers again, in the extreme south in June, and spreads to the Hull-Bremen and Hull-Copenhagen routes in July as might be expected from Graham's (1948, pp. 80-81) observations on summer spawning of cod. *Onos cimbrius* occurs with greatest frequency in these two months. In August there is a marked decline in numbers of young *Gadus* spp. It is worth noting that haddock was found once in this month, on the Aberdeen to Lerwick route. Single specimens of hake were taken off the Skagerrak in August and in September.

The patches of cod and whiting in the Southern Bight, which extend later to the Heligoland Bight, are the most important of the spring period (January to April) and this distribution is in reasonable accord with that given by Heincke (1905) and Redeke (1907), and fits satisfactorily with the distributions (up to mid-March) shown by Simpson (1948, 1949). It seems reasonable to suggest that these young cod, with those recorded from the central part of the Hull-Bremen route, originate from the early spawning in this area. Those occurring further west, off the Humber, can more readily be related to the "off Flamborough" spawning area (Graham, 1948), while the patch off the Firth of Forth, and the occurrences over the central section of the Hull-Copenhagen route, would seem more likely to be related to the spawning areas further north, particularly that of the "Forties" (Graham, 1948, Fig. 5) from which the young have been carried southwards in the surface currents (Böhnecke, 1922, and Tait, 1937). The small spawning of cod in the summer months appears to be centred in the Southern Bight and to extend only a little way north.

<sup>1</sup> The majority of these haddock were found in 1947, but they were noted occasionally in these months in other years.



From May onwards whiting are spread over almost the whole area. The occurrences of haddock from March to July suggest some relationship with the current system of, and to, the Fisher Bank, but the numbers are very small, so this possibility cannot be confirmed from our material. It is, however, in accord with the statement on haddock in Vol. X of the 'Rapports et Proces Verbaux' (Anon., 1908, p.54) that there is "a great deal (*of spawning*) on the Ling Bank and Great Fisher Bank".

The spawning areas of the saithe are shown in Fig. 13 of the same report as being limited to the deeper waters well to the north, so that the occurrences in our records of young so far south in March, April and May can only be explained on the assumption that they have been carried down the east coasts of Scotland and England by that part of the North Sea circulation which turns to the north-east at about the level of the Wash (see Böhnecke, 1922, Fig. 18) and which does not become included in the Dogger Bank circulation. The records of O-group stages also shown in the figure quoted (Anon., 1908) off the southern Danish coast (and off the Tyne) offer some support at least for this suggestion. (See also p. 80 (Anon., 1908) where it is stated that young may be found in the south of the area.)

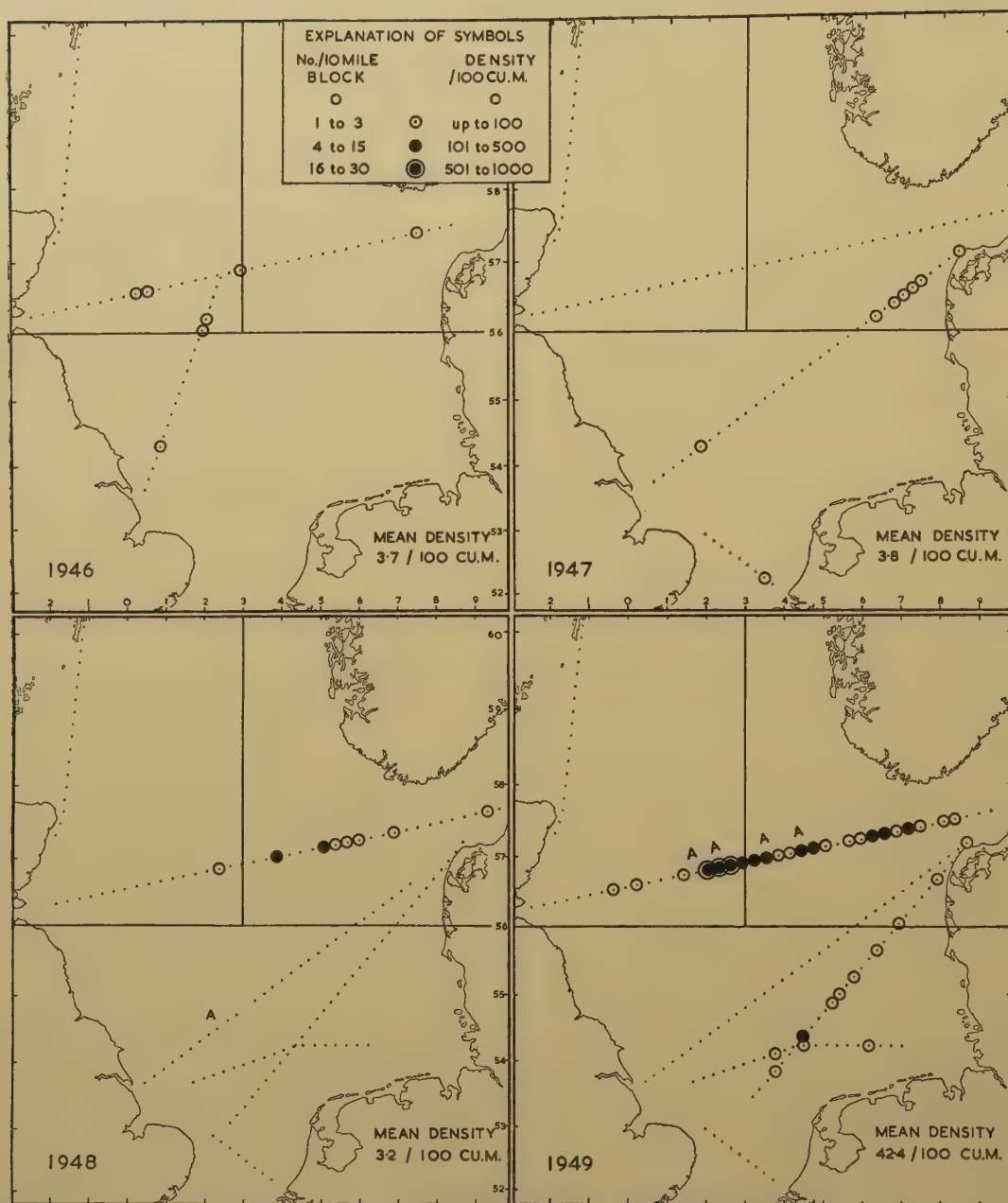
The position of the spawning areas, and the known abundance of this species in the northern North Sea, would have led one to expect appreciably greater numbers of the young in the recorder material than have actually been found. The sampling in this area, however, depends on the routes from (a) Leith to Copenhagen, where young saithe were found off the Firth of Forth, (b) the Pentland Firth to Bergen, where few Gadoids were taken before April on the few records available, and (c) Aberdeen to Lerwick, where the numbers of young fish caught are exceptionally low except where the track has crossed concentrations of newly hatched herring. Over a period of six years the total of young gadoids is only 56, and *G. virens* was not identified among these. *G. esmarki* was not represented either. As both these species have been identified with some regularity from the inshore ends of the Atlantic routes, it can only be assumed that on this route the young were not present at the 10 metre level of sampling in sufficient numbers to have been captured.<sup>1</sup>

There is a fair consistency in the occurrence of *Onos cimbrius* from April onwards, with June and July the months of most frequent records. The majority are found on or to the south-east of the Hull-Copenhagen route, particularly on its south-western third, and on the Hull-Bremen route as far as Terschelling (see chart for June in Plate XXVI). The remaining species recorded have occurred only in small numbers, some very rarely, and thus support no useful conclusions.

(e) *Scombridae*.

In the post-war period young *Scomber scombrus* have been recorded from the

<sup>1</sup> Some contemporary investigations in connection with herring-plankton relationships have been carried out in the area of, and to the eastward of, the Aberdeen-Lerwick route. The results of the plankton sampling, carried out in this case with the Small Plankton Indicator, suggest that young saithe are more frequently found at the 10 metre level well to the eastward of the Aberdeen-Lerwick route.



TEXT-FIG. 3.—Charts showing the distribution of young *Scomber scombrus* in July of the years 1946 to 1949, and in August of 1948 and 1949, in the North Sea. The letter A shown above the line indicates the positions of occurrence in August on the 1948 and 1949 charts. Overall mean densities per 100 cu.m. for July only are shown in the right-hand bottom corners of each chart.

North Sea, mainly to the north of  $56^{\circ} 00'$  N. latitude, in numbers which were very much greater in 1949 than in the preceding years. These young occurred mainly in July, but a few were found in August of 1948 and 1949. The series of charts in Text-fig. 3 show the distribution in the years concerned and inset figures are added to indicate the mean densities per 100 cubic metres which were attained. Although in the north-east there was an increase from 1946 to 1947 and 1948 and then to 1949, this sequence of events is not repeated in the other areas, and the average density for the whole area varies little from 1946 to 1948, but then increases to a very high value. It must be noted, however, that the figures for 1946 may be lower than they should be, due to the limited number of records, but this limitation does not apply to 1947 and 1948. Fraser (1949), p. 83 and Saville (1950), p. 101, found 1947 a better year than 1948, but 1949 better than either of the earlier two. These records are mainly further to the north and west than ours, so it is rather difficult to obtain a direct comparison, but the two sets of results are in reasonable agreement.

#### DISTRIBUTION AND IDENTITY OF THE FISH EGGS

Fish eggs are recorded in all months from January to August, although in these two months the numbers may often be small; their occurrence after August is, however, negligible.<sup>1</sup> Stubbings (1951) shows on Plates CIX to CXI the distribution of fish eggs month by month for the years 1932-39 and a comparable series of charts for 1946-49 (not figured) indicates generally similar distributions. In the earlier years it was only in 1933 and 1934 that appreciable numbers were found in January, and in 1935 the numbers remained low until March. February was characterized by appreciable numbers and a wide distribution except in 1935. In the 1946-49 period, however, there were patches in the south-east in January of all years (except 1946 when the southern routes were not available) and the February and March distributions were generally similar to those of the earlier years. In the charts for 1932-39 some dense concentrations of eggs occurred over the centre of the North Sea in July, 1937, June and July, 1938 and June, 1939. Comparable densities are found in 1946 and 1947, but the numbers are much lower in 1948, and lower still in 1949.

In Plates XX and XXIV the average numbers of fish eggs caught per 10-mile block are shown for the months January to August, the figures being derived from all the available records from routes regularly operated in the North Sea. There are two important periods of egg production in the year, February-March and June-July. The former may be preceded by small concentrations in the south-east in January, and followed by a persistence of the patches into April in the north. The January patch, when present, is clearly defined and limited to the south-eastern end of the Hull-Rotterdam route. April concentrations, when present, are seen off the east Scottish coasts and at the entrance to the Skagerrak. In February and

<sup>1</sup> Since the survey commenced only 21 eggs have been taken in the period September to December inclusive.



March the eggs are more widely distributed and the numbers are higher, but the greatest densities lie mainly in the south and east, from the Flemish Bight round into the Heligoland Bight. Apart from one or two small local patches, most often seen in the north, fish eggs are scarce in April and May, although the spread is fairly uniform, and there is no advance indication of the second "peak" of production which occurs in June. In this month densities are high over most of the area, highest in the central and northern regions, and generally lowest in the south-east. Most of these concentrations persist into July, although the numbers decrease considerably, often to about a third of the June level, and by August only a few scattered traces of the densest June-July patches remain. This seasonal sequence of changes in abundance may be seen, with only minor variations, in each of the years over which the survey has extended.

Although relatively few of the eggs in our material have been identified, circumstantial evidence based on the larvae found at the same time or immediately afterwards, suggests the probable identity of the main concentrations. These inferences can be related to the results of earlier workers, and to some contemporary results from the southern part of the area.

The early peak in the southern part of the area, which is first evident in January, at the south-east end of the Hull-Rotterdam route, and which then spreads northwards and eastwards round into the Heligoland Bight throughout February and March, comprises the eggs of plaice and cod initially. Later, eggs of whiting are soon added, followed by those of dab which increase in proportion as those of plaice diminish. Reference to authorities on the spawning periods of these species shows that plaice spawning may be well advanced by December<sup>1</sup> (Lee, 1909, p. 103) but that it is at its height by the end of January and the beginning of February (Buchanan-Wollaston, 1915, p. 12) and is almost over by the beginning of March. The plaice spawning grounds given by Masterman (1911, p. 22, and Plate) are all sampled to some extent by the recorder routes, so that plaice eggs might be expected to form a large part of this early peak. They have not, however, been so commonly noted in our records as to account for this peak in its entirety, as some other species have been identified, and of the remainder very few could be ascribed to plaice, on grounds of size alone.

Redeke (1907, p. 7) and Heincke (1905, p. 25) show that the eggs of cod and whiting occur off the Belgian and Dutch coasts from January to March, and that whiting spawns extensively to the south and east of the Dogger Bank. According to Ehrenbaum (1927) the dab spawns throughout the North Sea from January to July, and Simpson (1948, 1949) finds many dab eggs among his catches from the southern North Sea in January and February. It appears likely also that there is some drift of the eggs of plaice and cod from the spawning area off Flamborough (Masterman, 1911, and Graham, 1948) on to the western end of the Hull-Copenhagen

<sup>1</sup> Only two fish eggs have been recorded in December since the survey commenced, one in 1932 and one, identified as plaice, in 1948. The sampling in this month has been fairly regular, so it seems probable that any December concentrations of plaice eggs in any of the other years were so situated that the Recorder routes did not sample them.

route, and perhaps also on to the western portion of the Hull-Bremen route, but the position of the main haddock spawning areas, all in the northern North Sea (Thompson, 1928, p. 78), suggests that it is unlikely that these eggs are represented. However, haddock eggs have been identified in February from the middle of the Hull-Copenhagen route, and on the Leith-Copenhagen route. According to Bowman (1914, 1921) one might well have expected to find plaice eggs off the Firth of Forth or the Aberdeenshire coast, but they have not occurred in our material. Cod should also have been fairly common over this route from February to April (Graham, 1948), but have not been noted as specially abundant.

After March there is a very marked decrease in the numbers of eggs; very few are found in April, hardly any in May.

The late peak of egg production in June and July builds up very suddenly; the only case of large numbers being obtained in May being from a record taken on the 30th and 31st of that month. It is clear, too, that this is essentially a short spawning period in which the eggs disappear very rapidly, as records taken late in July seldom have many on them. The densest patches occur in the central and northern parts of the area, those in the south and east being relatively small.

On the limited evidence of eggs identified in the Recorder material, it would appear that the eggs of dab and whiting are still relatively common over the whole area during the June-July period. It also seems probable that in some years haddock eggs were present, otherwise it would be difficult to account for the captures of young haddock, of the order of 5 to 8 mm. in length, in June of 1947, and in July of 1946, 1947 and 1948. Plaice eggs are only rarely found, sometimes off the Firth of Forth, as might be expected from the observations of Fulton (1907, p. 338), and sometimes off the Baltic. The few cod noted are from the southern part of the area (see p. 226). There are small numbers of the other species of *Pleuronectes*, and of the common sole. Of the other *Gadidae*, *G. esmarki* and *G. minutus* occur in small numbers over the whole area. It appears likely that mackerel eggs are abundant on the Leith-Copenhagen route, and perhaps the Hull-Copenhagen route also, although none have been identified, as the larvae were found in exceptional numbers in 1948 and 1949. It is probable too that the eggs of the sprat have contributed appreciable numbers to the concentrations further to the south and east (see p. 223 above) particularly in June and early July.

### YOUNG FISH AND FISH EGGS OF THE ATLANTIC ROUTES.

The Atlantic routes, which have been operated by ships of the Ocean Weather Service sailing from the Clyde, provide records over the years 1948 and 1949, a period rather too short to give reliable indications of seasonal fluctuations. It is evident from the material available, however, that on these routes separate populations are sampled, the boundary between which approximates closely to the point at which the routes cross the 100 fathom depth contour. The species taken from the inshore sections, and the changes in their numbers, are in many respects



similar to the results determined for the North Sea. Such variations as have been noted in the results so far available are no greater than may be seen in different parts of the North Sea. Offshore, over the deeper water, there are marked differences, but the data available are insufficient as yet to indicate the seasonal fluctuations for the young fish. The differences between the populations of the inshore sections and those found over the deeper waters offshore are, however, discussed for a number of other forms (for example, *Tomopteris*, *Thaliacea* and *Euchaeta spp.*) by Rae (1949, 1950, 1951 and 1952), for the period 1948 to 1951.

The fish eggs from the inshore sections of these routes occur from February to August only, and have been of most frequent occurrence in March and in May. A peak in March coincided in time with that found in the North Sea, but a May peak is a month earlier than that in the North Sea, where it occurs in June. Hardly any fish eggs were recorded from over the deeper waters.

Young Clupeidae, among which only *Clupea harengus* has been identified, have occurred with some regularity but seldom in large numbers, off the north and north-west coasts of Ireland in November and December of 1947, 1948 and 1949 and to the north and north-west of the Butt of Lewis in the same months of 1947.<sup>1</sup> A few individuals, generally larger in size, were recorded from the same areas in February of 1948 and 1949. These records seem to be in reasonable agreement with distributions which might be expected following the spawning of September and October as shown in the 'Herring Atlas' (1950) for these areas. A few individuals of small size, widely scattered, were taken west of the Hebrides in April-May, 1948, and March-April, 1949. At present the evidence is insufficient to suggest their origin.

*Ammodytes spp.* were recorded from the inshore sections of the Atlantic routes in March and April, and in July, August and September. The majority of the occurrences were from the shallowest waters within the 100 fathom line. The records from March and April indicate a rather limited distribution, spreading outwards from the coasts as in the North Sea, and the largest numbers were found in April. This agrees with the timing of the "spring" peaks in the North Sea, particularly that of the north-western area (Text-fig. 6). The occurrences during the July to September period are widely scattered, and the numbers are low. These conditions are similar to those found in the North Sea at this time of the year, but the absence of *Ammodytes* in the records from the Atlantic routes in May and June suggests a more distinct separation between the "spring" and "summer" peaks than was seen in the North Sea material.

Hardly any Pleuronectidae have been found on the Atlantic routes, but four out of the total of five identified are *Pleuronectes platessa* or *Pl. limanda* from within the 100 fathom line north of Ireland, in March and April.

The Gadidae are more numerous, and from the shallower sections of the routes the following are recorded, mainly from the area north-west of Ireland.

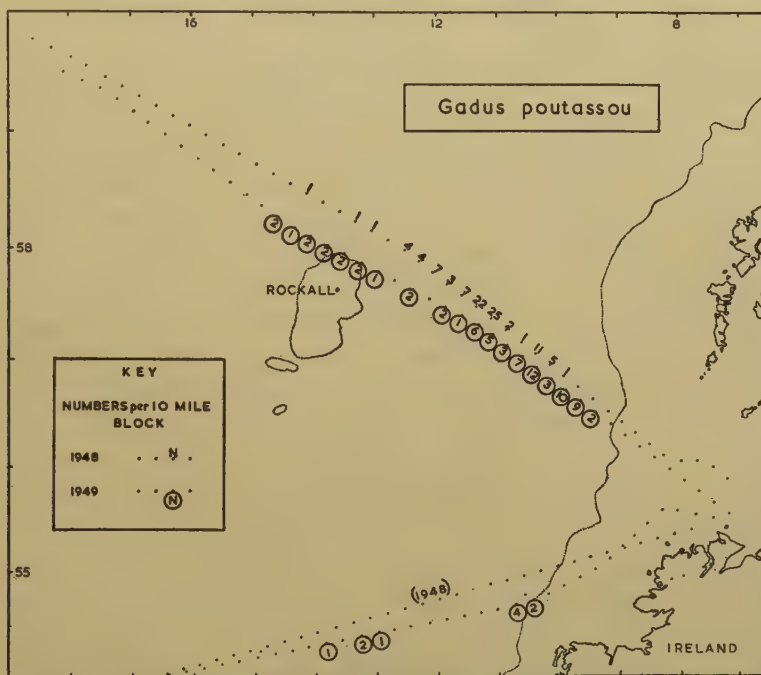
<sup>1</sup> Sampling on this route was not available in late 1948 and in 1949, but has been resumed in 1950.



| February.        | March.               | April.               | May.                 | June.               |
|------------------|----------------------|----------------------|----------------------|---------------------|
| <i>G. virens</i> | <i>G. virens</i>     | —                    | —                    | —                   |
| —                | <i>G. aeglefinus</i> | <i>G. aeglefinus</i> | <i>G. aeglefinus</i> | —                   |
| —                | <i>G. pollachius</i> | <i>G. pollachius</i> | —                    | —                   |
| —                | <i>G. minutus</i>    | <i>G. minutus</i>    | —                    | —                   |
| —                | —                    | <i>G. merlangus</i>  | —                    | <i>G. merlangus</i> |

The offshore limit of the distribution of these species, particularly of *Gadus virens*, is less sharply defined than that seen in the other groups, and individuals have been taken over deep water as much as 30 to 50 miles outside the 100 fathom line.

Large catches of young *G. poutassou* were recorded, over deep water, from the northern route in April of both 1948 and 1949. These extended over 150 to 200



TEXT-FIG. 4.—Chart showing the distribution of young *Gadus poutassou* on two Atlantic routes in April of 1948 and 1949. The figures show the actual numbers caught per 10 mile block or approximately 3 cu.m. of water filtered.

miles of the route, the western limit of distribution being in the vicinity of Rockall Bank. The eastern limit was outside the 100 fathom line. The numbers were high, ranging up to 25 per 10-mile block (equivalent to a density of 8.33 per cu.m.) and these larvae were more abundant in 1948 than in 1949,<sup>1</sup> although in 1949 the patch was more widely spread.

The distribution in 1948 and 1949, shown in Text-fig. 4, appears to be less

<sup>1</sup> 1948: 93 caught in 150 miles of route, mean density 2.17 per cu.m. 1949: 72 caught in 200 miles of route, mean density 1.2 per cu.m.

extensive and to cover a shorter period than that given by Schmidt (1905, pp. 61, 62; 1906, p. 12). The recorder material, however, is limited to the single depth of 10 metres, at which the range of sizes caught is restricted to specimens from 5 to 10 mm. in length. Unfortunately, the sampling on the Pentland Firth-Iceland route was insufficient in 1948 and 1949 to show the details of the contemporary distribution in the areas south of Iceland and off the Butt of Lewis, so preventing adequate comparisons with the distribution as shown by the "Thor" collections.

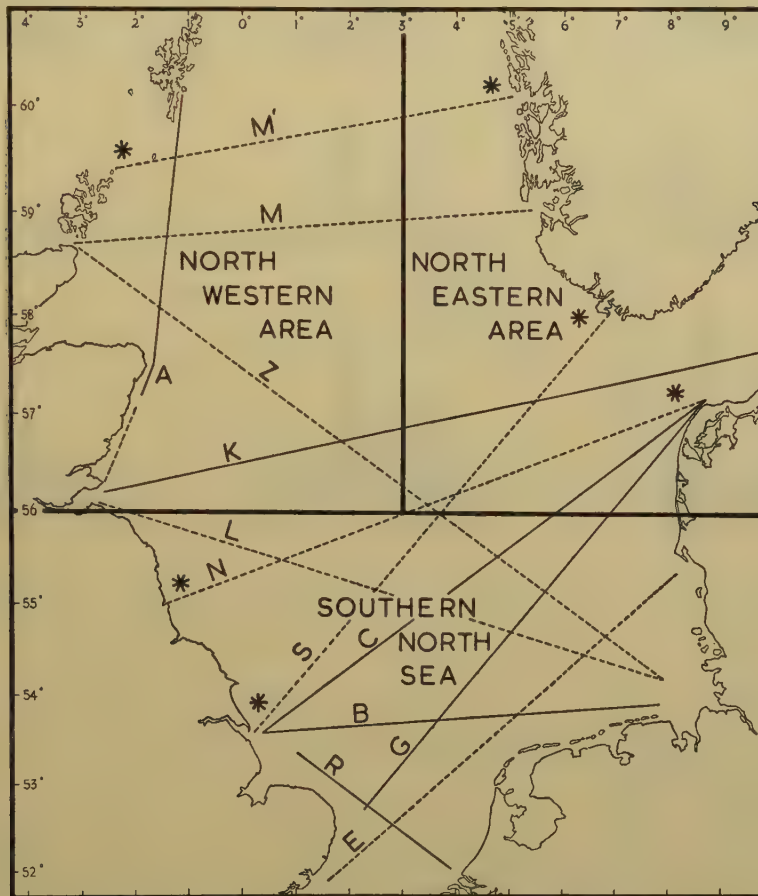
Our records of young *G. poutassou* on the Atlantic route from the Clyde to Station "I" only extended as far as 15° W. long., although the sampling continued beyond the westerly limit (19° 05' W. long.) of the "Thor" catches. None of our catches were taken from waters within the 100 fathom contour. In the area south of Iceland there was only one record, in May, 1948 (see Rae, 1952, Plate XIII, 23V) which afforded any information. On this some *Gadus* spp. were taken, ranging from 5 to 12 mm. in size. Their specific identification was uncertain, as all were badly crushed, but a few were tentatively ascribed to *G. poutassou*. These few occurred more or less together, from approximately 60° 45' N., 15° W. to 62° N., 18° W. The presence of young *G. poutassou* in this area would agree with the distribution shown by Schmidt. Writing on *G. poutassou*, Hickling (1928) said that "the greatest concentrations of ripe females are found in March and April to the north-west of Cape Wrath outside the 100 fathom line." This area was not sampled by the Recorder in 1948 and 1949, but in 1939 two records were taken which cut right across it. One was in April, and caught no young *G. poutassou*, but on the May record they were recorded, in densities of 0.3 to 1.0 per cu.m., from 59° 45' N., 06° 45' W. to 61° 45' N., 13° 30' W. The size range was from 5 to 12 mm., and there was a gap in the sequence of occurrences where the route passed between Faroe Bank and Bill Bailey's Bank, over water of from 100 to 200 fathoms in depth. The overall density was approximately 0.3 per cu.m., about one-quarter of the 1949 figure for the Atlantic route.

It appears, on the basis of the recorder material, that the spawning commences quite suddenly, and is of relatively short duration. Our records of young *G. poutassou*, none of which have been larger than 12 mm., are limited to April and May. Very few of the April records are of specimens any bigger than 7 mm., although the largest numbers of individuals were found in this month. The absence of larger individuals, and indeed of any specimens after May, might perhaps have been expected in the light of the statement by Schmidt (1905, p. 62) that the young fish inhabit deeper layers as their size increases.

Outside the 100 fathom line the few fish eggs recorded are found from February to June, but most occurred in March and May. The young fish were most numerous from April to August, April-May-June and August being the months of most frequent captures. The April figures are dominated by the large patches of *Gadus poutassou*, of which some persisted into May, but in June and August the scopelid fishes contributed a large share of the totals. When further material is available the seasonal succession should become more clearly defined.

## SEASONAL FLUCTUATIONS IN THE NUMBERS OF YOUNG FISH AND FISH EGGS.

From the accumulated data provided by our records the changes in abundance from month to month of the fish eggs and the different groups of young fish can be studied, and for this purpose it has been found convenient to divide the North Sea

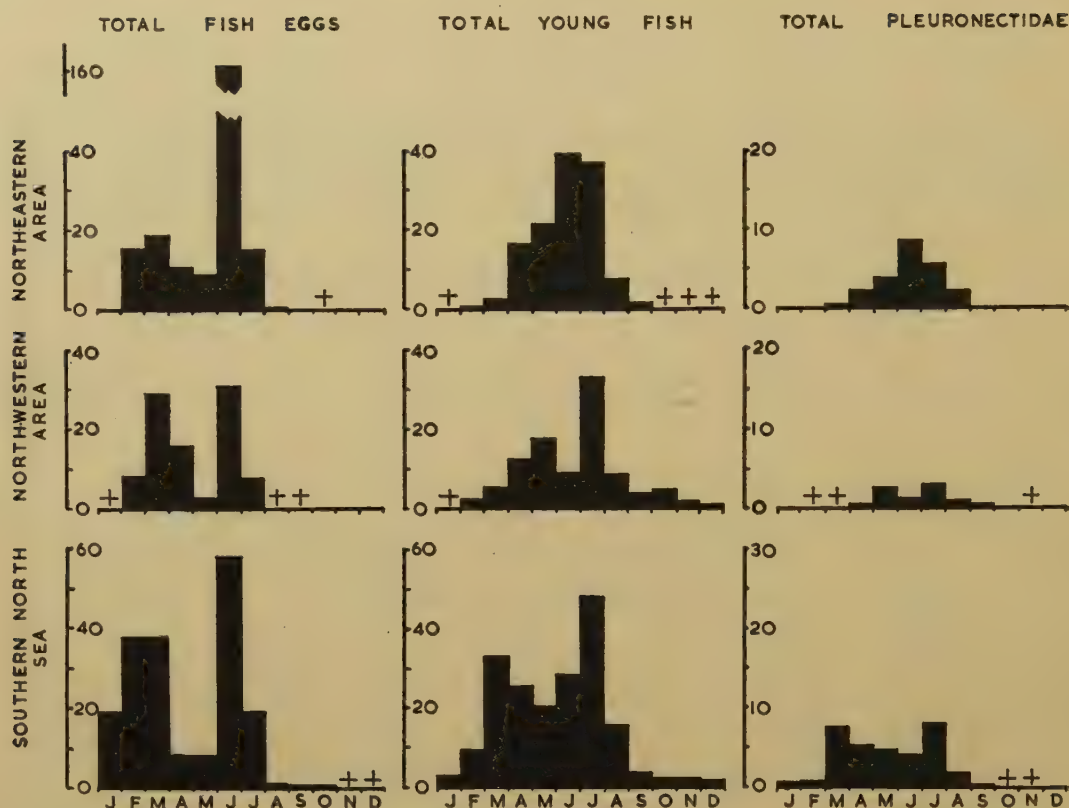


TEXT-FIG. 5.—Chart showing the recorder routes in the North Sea and the three areas used in computing the histograms in Text-figs. 6 and 7. Routes sampled regularly are drawn with a continuous line, whereas those which were discontinued after 1939 or which were only operated occasionally are shown by a broken line (see also p. 217).

into regions. The boundaries of these regions, the southern North Sea, the north-western area, and the north-eastern area are shown in Text-fig. 5, where the extent of the sampling is also indicated by the insertion of the routes regularly operated.

In Text-fig. 6 series of histograms are shown which depict the mean densities per 100 cu.m. sampled for each month in the year for total fish eggs, total young



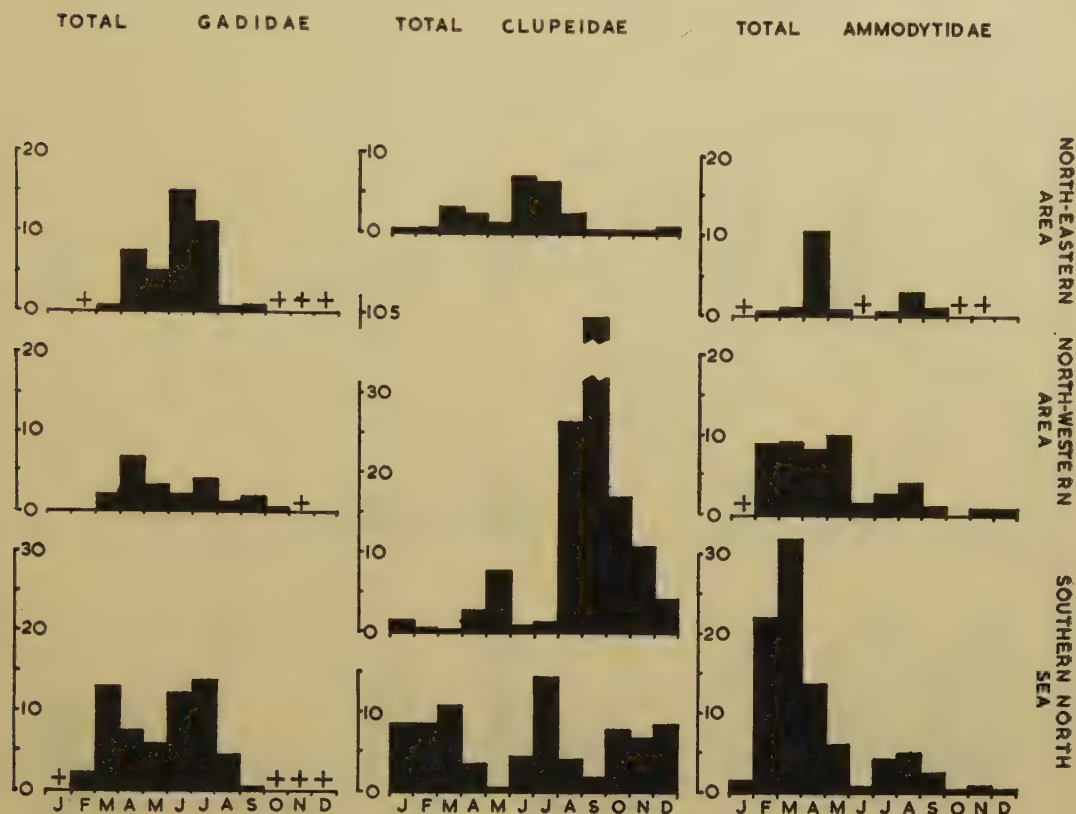


TEXT-FIG. 6.—Histograms showing the seasonal fluctuations in numbers of young fish and fish eggs in each of the three areas in the North Sea (see Text-fig. 5). The scales give the mean density per 100 cu.m. for each month, determined from all the data available

fish (excluding Clupeidae and Ammodytidae), total Pleuronectidae, total Gadidae, total Clupeidae and total Ammodytidae. Separate histograms are shown for each of the three areas treated.

These histograms show mean figures which have been smoothed to some extent as a result of averaging, but it must be emphasized that the same basic pattern of succession can be seen in the results for any individual year. The variations which occur from year to year affect the general level of abundance rather than the sequence of seasonal changes.

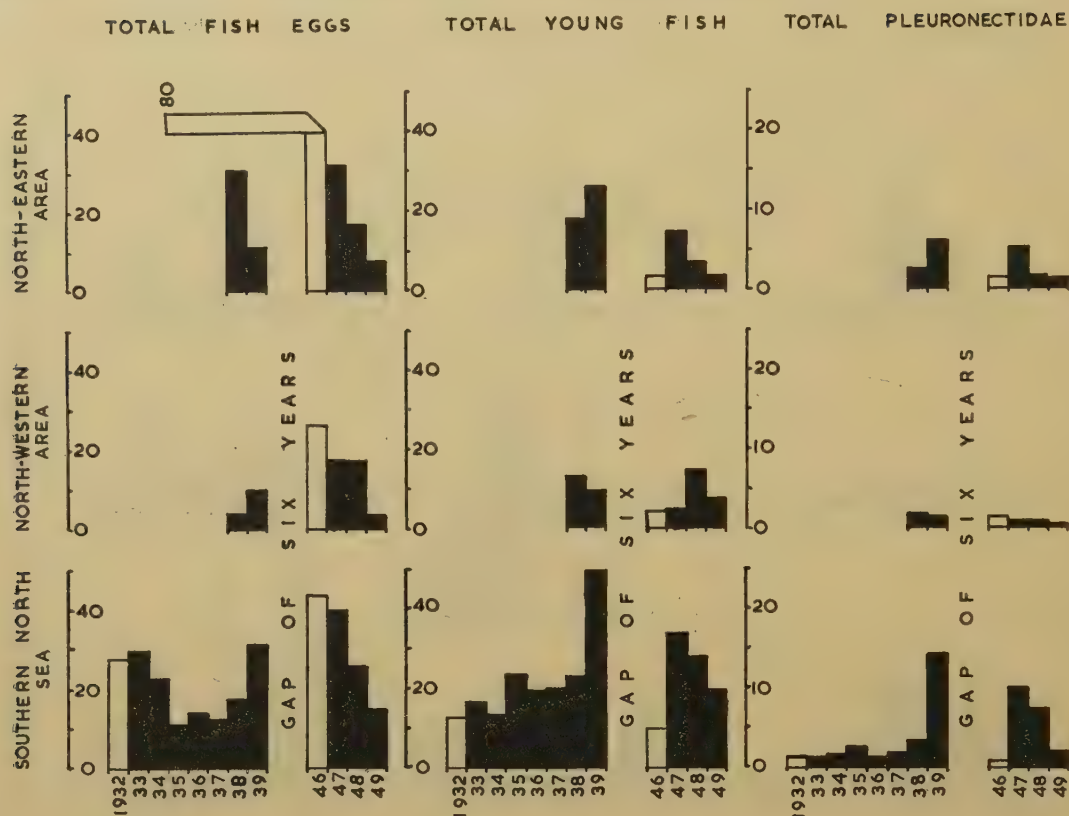
The patterns of succession for each group in the southern North Sea and in the north-western area are very similar in general appearance. Characteristically they show an early or "spring" peak in numbers, most marked in the fish eggs and in general more clearly defined in the southern North Sea; which is followed by a diminution in numbers until June–July, when a second, or "summer," peak occurs, and in many cases reaches higher levels than the early peak, but is more limited in time, falling in June for fish eggs and in July for the young fish generally. The "spring" peak appears to build up and fall off somewhat earlier in the southern



from 1932-39 and 1946-49. The histograms in the column headed Total Young Fish exclude the Clupeidae and the Ammodytidae.

North Sea than in the north-western area, where it may not reach its maximum until May for some groups, whereas in the southern North Sea the peak is always attained by March. The second peak was found in June (for eggs) or July (for young fish) in all the areas, whether the corresponding early peak was in March or in May. In the Ammodytidae alone the "summer" peak occurred in August, preceded by a high July value in the southern North Sea only. In this group the "spring" peak extends over three or four months in the southern North Sea and the north-western area, but occurred relatively late, in April, in the north-eastern area.

In the north-eastern area the histograms for fish eggs and for the Ammodytidae show the two peaks characteristic of the other areas, although the diminution in egg densities after March is relatively much less; but in the remaining groups there appears to be a continuous build-up of numbers from March to June, followed by a July figure only slightly less than that for June, then the drop to a low value in August. The early peak in the southern North Sea includes relatively large components of plaice and cod, and although plaice is relatively less common in the



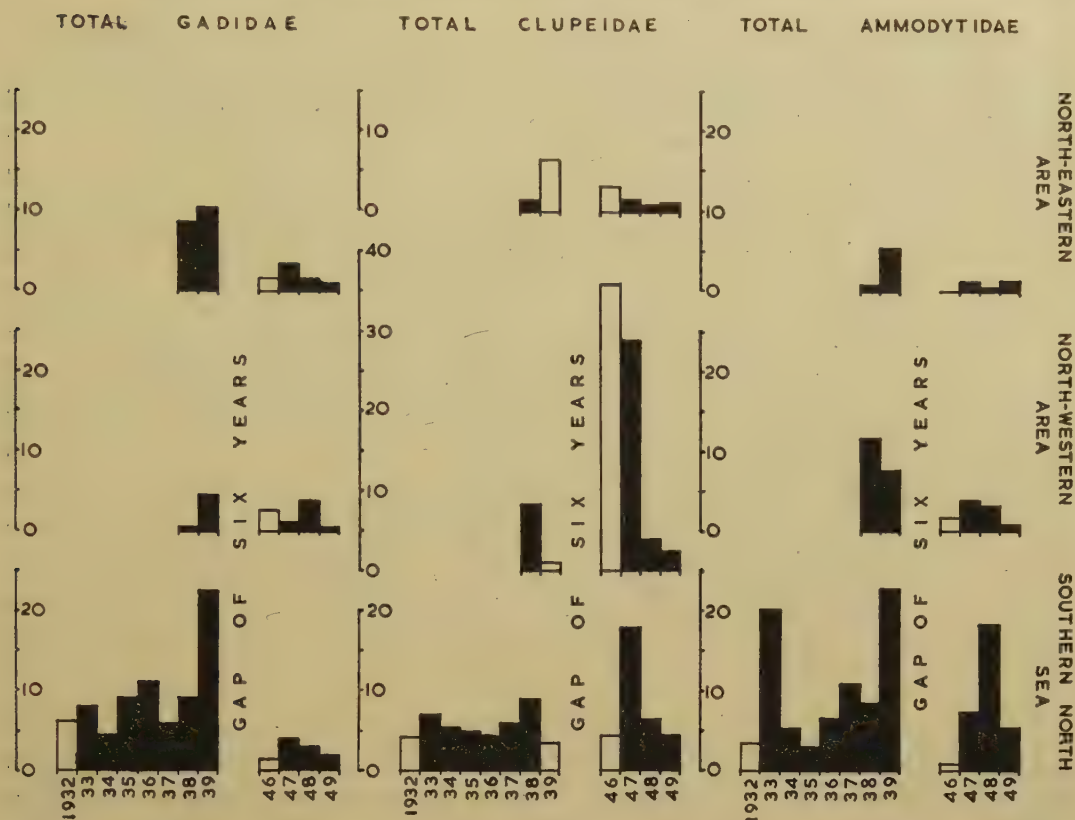
TEXT-FIG. 7.—Histograms showing the annual fluctuations in numbers of young fish and fish eggs in each of the three areas of the North Sea (see Text-fig. 5). The scales give the mean density per 100 cu.m. per month for each year, determined from the data for the months January to August inclusive, except for the *Ammodytidae* where

north-western area (Bowman, 1914, 1921) cod is still important and contributes significant numbers in the "spring" months, supported by saithe, thus producing an early peak in this area similar to that in the southern North Sea. On the other hand, the occurrences of these species in our records from the north-eastern area are relatively few, and the single peak, which attains its maximum in June, contains comparatively large numbers of haddock and dab, which do not appear so early in the season in this area. However, except in the north-eastern area, there appears to be a distinct "pause" in the spawnings occurring during the course of the year, as some species, for example whiting, which were recorded in all months and were abundant in the "spring" peak, become numerous again in the "summer" peak.

#### ANNUAL FLUCTUATIONS IN THE NUMBERS OF YOUNG FISH AND FISH EGGS.

It became evident quite early in the course of the survey that there were marked differences from one year to another in the numbers of fish eggs and young





September is included, and for the Clupeidae, where all twelve months are used. Open histograms are shown for the years in which the sampling was limited. The column for Total Young Fish does not include the Clupeidae or Ammodytidae or *Scomber scombrus*.

fish, discernible from even a cursory inspection of the plotted distributions,<sup>1</sup> and justifying a more precise evaluation than could be assessed from the charts. So, for each year of the survey, and for the separate areas (p. 235) where appropriate, a figure has been derived to express the mean monthly density (per 100 cubic metres) for the fish eggs and the several groups of young fish. These figures are based on the data for the months January to August for all groups except the Ammodytidae, where September is added, and the Clupeidae, where all twelve months are included to cover the late spawning. The results from two of the years must be treated with caution; in 1932 records were not available until June, while in 1946 the sampling was restricted, and several important routes were not sampled until October (see charts, Rae, 1952). In 1939 there were no records after August, so that, although the results for all the other groups were unaffected, the figures for the Clupeidae do not include any sampling of the later spawners, and so must be treated as only partially complete for this year.

<sup>1</sup> See Stubbings, 1951; e.g. compare March and April, 1937, on Plate CXXIII with March and April, 1939, on Plate CXXIV.

The fluctuations in numbers from year to year are shown for all the groups studied, for each of these areas, in Text-fig. 7. For the years up to 1939 the majority of the data relates to the southern North Sea, and it is convenient to state first the main features of the results from this area :

- (i) There is a marked trough in the graph for numbers of fish eggs, occurring in the years 1935 to 1937, with a subsequent recovery in 1938 and 1939 to a level similar to that prevailing in 1933-34.
- (ii) In the case of the graphs for total young fish (less Clupeidae and Ammodytidae), total Pleuronectidae and total Gadidae, a generally rising trend is evident, interrupted by a slight check in 1934 (not seen in the Pleuronectidae), and a further check in 1936 and 1937 (but 1937-38 for the Gadidae). In all cases, the figure for 1939 is very much higher than that for any of the preceding years.
- (iii) The numbers of Clupeidae fall slightly from 1933 to 1936, and then increase again up to 1938. The 1939 figure is not representative as there was no sampling in the autumn. The numbers of Ammodytidae are much lower in 1934 and 1935 than they were in 1933, but there is then a steady increase in numbers up to 1939, when the level is similar to that of 1933.

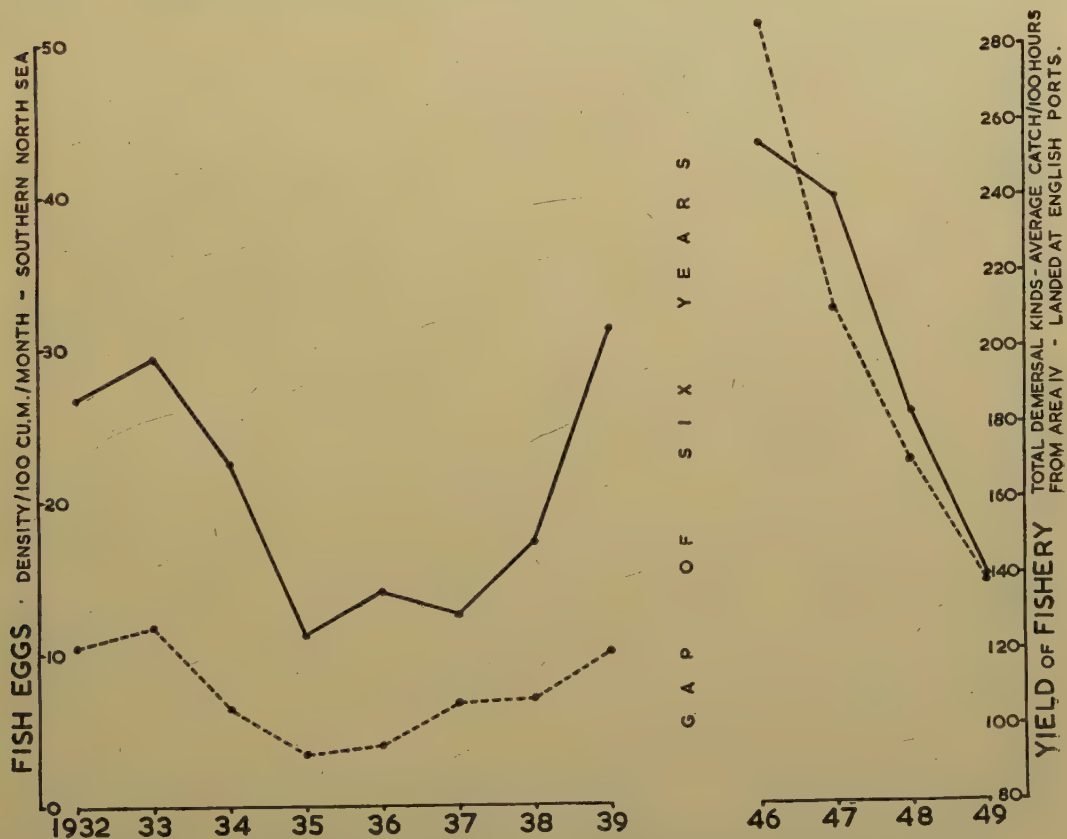
In the post-war period of 1946 to 1949 the most outstanding feature is the marked decline in numbers from 1946-47 to 1949 for all groups except the Ammodytidae and one other species, *Scomber scombrus*. There are some minor inconsistencies of detail, arising mainly out of differences between 1946 and 1947, which are probably due to the deficiencies of sampling in 1946,<sup>1</sup> but the figures leave little doubt that the decline in numbers in the immediate post-war years applied to practically all the young fish, and affected the whole area. The magnitude of the decline may be appreciated when it is seen that the numbers in 1946-47 were in some cases 3 to 5 times as great as those determined for 1949. The fluctuations in the numbers of Ammodytidae in the southern area do not conform to the trend seen in all the other groups, the numbers increasing up to 1948, but there is then a decline to a low level of abundance in 1949. On the other hand, *Scomber scombrus* (see p. 227 and Text-fig. 3) is the exception, in that the numbers recorded have increased from 1946 to 1949, and were exceptionally high in the July of 1949. In the period up to 1939 they had not been recorded at all, as may be seen from the list of species in Stubbings' account (1951, p. 278). Many of the records of this species occurred on the Leith-Copenhagen route, however, and if they had been less common in 1938 and 1939 than they were in 1946, then they might not have been included among the relatively small numbers of young fish obtained from this route in July in either 1938 or 1939 (see Stubbings, 1951, Plate CXIV).

<sup>1</sup> Possible corrections for incomplete sampling which have been tested indicate the probability that all the figures for 1946 should be higher, but none appear of sufficient reliability to justify their application.

### FLUCTUATIONS IN ABUNDANCE OF YOUNG FISH AND FISH EGGS IN RELATION TO THE YIELD OF THE FISHERIES.

The data from the recorder survey, although limited to the standard depth of sampling of 10 metres, provides an opportunity of comparing the numbers of young fish and fish eggs before and after a "close time" for commercial fishing comparable with that which occurred from 1914 to 1918, although longer and almost certainly much more widespread in its effects ('Report on Fisheries of Scotland, 1939-1948,' para. 5, pp. 11, 12, 1949).

In the light of the statement by Buchanan-Wollaston (1926, p. 6) that "An estimate of egg production in a certain area is undoubtedly the most reliable criterion of the extent of the stock producing them . . . ," it seems desirable to examine first the relation between the fluctuations from year to year in the numbers of fish eggs in our records and the yield of the fisheries over the same period, in order to determine whether this statement can be applied over a large area for a number of species combined.



TXET-FIG. 8.—A comparison between the number of fish eggs taken by the recorder in the southern North Sea (solid line) and the commercial landings at British ports by boats fishing in Area IV (broken line) from 1932-39 and 1946-49.



Up to 1937 the recorder sampling was confined to the southern North Sea, so the figures for this area only can be used for this comparison. In Text-fig. 8 the densities of fish eggs taken by the recorder in the southern North Sea, expressed as mean densities/100 cu.m./month for each year, are compared with the corresponding catches of all demersal fish in cwt. per 100 hours fishing, in the North Sea (Region IV<sup>1</sup>), landed at English ports by British boats. Foreign catches and landings are not included, but this should not be a serious limitation, in view of the large part played by British vessels in this area.

The fish egg densities at 10 metres, comprising the summed figures for all species, appear to fluctuate in very close conformity with the catches of total demersal species expressed as quantities per unit fishing effort. It appears that in the two or three years prior to the war there was a slight improvement in the stock, if the catch per unit effort may be taken as a measure of this, while the increase in the fish egg density is certainly in complete agreement with this upward trend. During the war period, with the level of fishing reduced to one which produced somewhere between one-third and one-half of the total landings of previous years, the stocks must have been greatly replenished, a point well confirmed by the reports on the effect of the war on the stocks of commercial fishes which make up Vol. CXXII of the 'Rapports et Proces Verbaux of the International Council for the Exploration of the Sea.' Of the individual reports those by Wimpenny (1948), Jensen (1948), Parrish (1948) and Margetts and Holt (1948) are the most relevant to the present consideration. The general increase in yield per unit effort, particularly in 1945 and 1946, is an added confirmation. These available, or catchable, stocks evidently decreased very rapidly, as the return per unit effort is halved (see English landings) between 1946 and 1949, reaching in the latter year a value only just above the pre-war figures. The decrease in the numbers of fish eggs in the same period is of the same order, at least twofold,<sup>2</sup> and by 1949 had reached a level comparable with that which occurred in the 1935 to 1937 period of low production.

This correspondence between the fluctuations in fish egg numbers and the yields of fish per unit fishing effort is evident in spite of the fact that all fish eggs are included without regard to their specific identity, whereas the yield includes only those species of fish which are of commercial value. On the assumption that the fish egg numbers are indicative of the strengths of the stocks producing them, one might have expected a significant contribution of fish eggs from the many non-commercial species in the sea. If the proportion of such eggs in the total was large, the relation between the numbers of fish eggs caught and the commercial yields might easily become obscured. This does not appear to have happened, and some possible explanations are suggested :

<sup>1</sup> Although the bulk of the catches were obtained from Regions IVa and IVb, there were some from IVc.

<sup>2</sup> Several methods of applying corrections for deficiencies in sampling were examined, although none appeared reliable enough to justify their use. However, all showed that in 1946 the actual figures would have been increased by between 20% and 50% by the application of any of the possible corrections.

- (i) The conditions of environment which influence the level of spawning activity may have affected all species in the same way, favourably or adversely, so that the sampling of any part of the stocks would show the same relation between eggs and yield.
- (ii) As such small parts of the recorder routes lie over the coastal waters where the eggs of coastal fishes (such as are planktonic) might be abundant, the catches of fish eggs may be roughly proportionate in their composition to the abundance of the commercial kinds of fish.
- (iii) The statistics show that four species of *Gadus* and four of *Pleuronectes* together make up 80% to 85% of the total demersal landings at Scottish ports, so that the relation between eggs and yield would be little affected even by catastrophic fluctuations in the spawning of the remaining kinds.
- (iv) The recorder might have caught the eggs of the most important kinds of commercial fishes to a proportionately greater extent than those of the other kinds. It may be significant that the eight species which together make up some 80% of the landings have eggs without oil globules, and that eggs with oil globules are relatively rare among those identified in the recorder material. One cannot entirely disregard the possibility that eggs with oil globules may have been most abundant nearer the surface than at the standard 10 metres at which the sampling takes place.

It is convenient at this point to see what relation, if any, exists between the fish egg and the young fish numbers. The histograms for the fish egg numbers from year to year may be compared with those for total young fish (excluding the Clupeidae and Ammodytidae and *Scomber scombrus*) in Text-fig. 7, where they are figured in adjacent columns. There is no evidence of a close correspondence between the two sets of histograms as the numbers of young fish show a generally rising trend from 1932 to 1939, while the fish eggs show a decline to a low level in 1935, 1936 and 1937, with a subsequent recovery. The increase in numbers of fish eggs from 1937 to 1939 is accompanied by an increase of approximately similar proportions of young fish, and after 1946 there is a steep decline in the numbers of both, but the trends of the changes up to 1935 appear to be opposed. This lack of correspondence between the young fish and the fish eggs might have been expected, in view of the impact of natural mortality at this stage of development. Indeed it is surprising to realize that the ratio of numbers of young fish/numbers of fish eggs for the individual years varied only between  $\times \frac{1}{2}$  and  $\times 2$  during the period covered.

It is now generally accepted that the first few weeks following the hatching of young fish must be a very critical period in relation to the contribution that the particular brood may make to the fishable stock in subsequent years. So far, however, in the experience of the many workers who have studied the problem, it has been exceptionally difficult to demonstrate any relationship between the abun-



dance of particular young fish and the yield of the corresponding adults. The material from the recorder survey does not offer much evidence in support of a relationship between young fish and subsequent yields. This might have been expected, for the comparison between the number of eggs spawned and the stocks of adult fish, as indicated by the commercial catches, is a contemporary one; while that between the number of eggs, or young fish, and the subsequent recruitment to the fishable stock is a long term one, in which the environmental conditions over several years can affect survival. It is, however, worth noting that the very marked increase in the numbers of total young Pleuronectidae in 1939 (Text-fig. 7) can be related to certain recorded facts. The success of this year class of plaice is stressed by Wimpenny (1947), and its strength in the sampling of the Waddensea grounds is noted by Taning (1943, 1947), while Jensen (1947) reports on an increased catch of North Sea plaice at Esbjerg in 1943.

It may be, then, that agreement between large numbers of larvae and the subsequent success of the year-class will only become evident when the brood strength exceeds some threshold value, above which the impact of natural mortality coupled with the incidence of unfavourable survival conditions will still be insufficient to prevent a good recruitment subsequently, but below which only the coincidence of favourable conditions throughout could ensure any measure of success.

Many writers have stressed the importance of the *Ammodytidae*, and Raitt (1934, p. 371) indicates the range of species of fish which, at least at times, depend on young *Ammodytes* spp. as a staple item of food. It seems important, therefore, to emphasize the wide range of fluctuations in numbers which occurred in the period covered by the survey (Text-fig. 7). There was a fairly consistent increase in mean density of young *Ammodytidae* from 1935 to 1939, which suggests the possibility that the stocks may have increased to some extent. Any such increase in the stocks of an important component in the diet of other fishes might have been a factor in relation to the survival of those of the food fishes which would contribute to the fishable population from 1940 onwards.

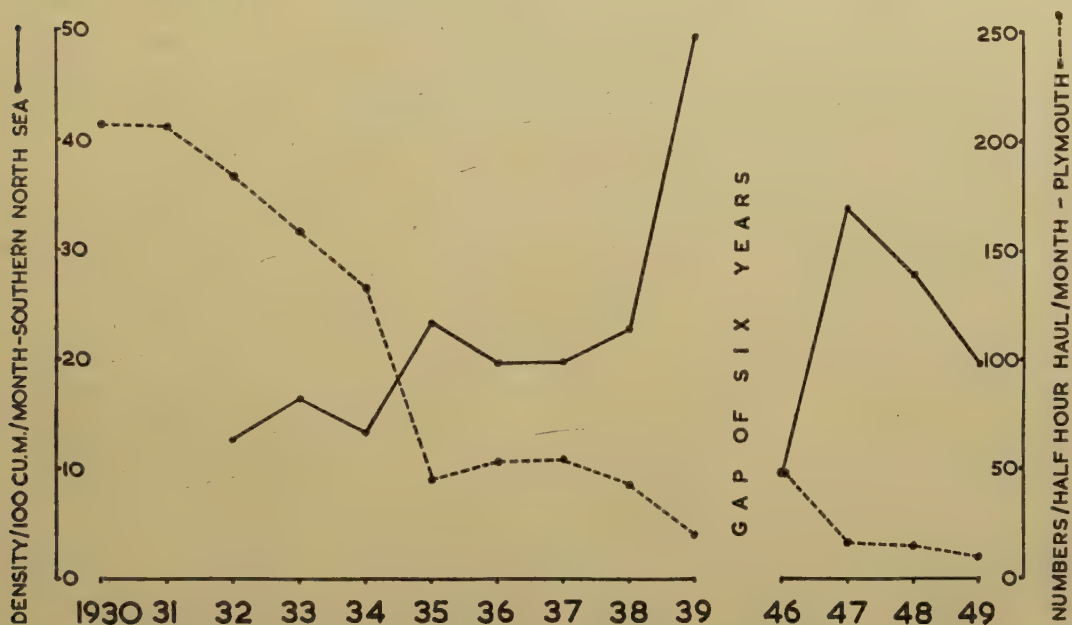
#### A COMPARISON WITH ENGLISH CHANNEL DATA.

In previous sections the seasonal and annual fluctuations in the numbers of young fish and fish eggs in the North Sea have been described. It seems appropriate at this point to compare the results from our work with those obtained by Russell (1930-1947) and Corbin (1948-1951) in the English Channel. Such comparisons cannot, however, be pressed too far, as in the Channel fluctuations in abundance at one station, 2 miles east of the Eddystone Light House, are considered, and the sampling is by a stepped, oblique haul from bottom to surface; whereas in the North Sea the sampling is widely spread over the whole area and is from a depth of 10 metres only. Therefore no detailed comparison of the seasonal successions are attempted.

If, however, the gross catches of young fish, expressed in convenient terms, are



compared over the years for which results are available, the trends of change in the average population in North Sea and Channel can be contrasted. In Text-fig. 9 for each year the results from the southern North Sea are plotted as numbers per 100 cubic metres sampled per month and the Channel results as mean numbers per half-hour haul per month, equivalent to about 4000 cu.m.<sup>1</sup> These two curves express the numbers of all young fish combined except the Clupeidae and Ammodytidae, and both are based on the period January to August in each year; after August the catches secured are insignificant.



TEXT-FIG. 9.—Graphs comparing the annual fluctuations in numbers of young fish, excluding the Clupeidae and Ammodytidae, taken by the recorder in the southern North Sea (solid line) and in tow-nettings at a point in the English Channel off Plymouth (broken line) for the years 1932–39 and 1946–49. The figures for 1946 are based on limited sampling in both areas.

It is evident that in the two areas the trends of the fluctuations in numbers were opposed up to 1939, that for the southern North Sea rising while that in the Channel was declining. Further, the minor fluctuations in individual years appear to occur in exact opposition to each other, most markedly in the years 1934–39. In 1936 and 1937 the only significant halt in the decline in the Channel is matched by a similar check in the increase in the southern North Sea, after which the general trends are resumed. From 1947 to 1949, however, there is a deviation from the pre-war trends as both are declining, although the North Sea curve is still at about the 1936–37 level while in the Channel the numbers have fallen still lower than they

<sup>1</sup> In a private communication from P. G. Corbin.

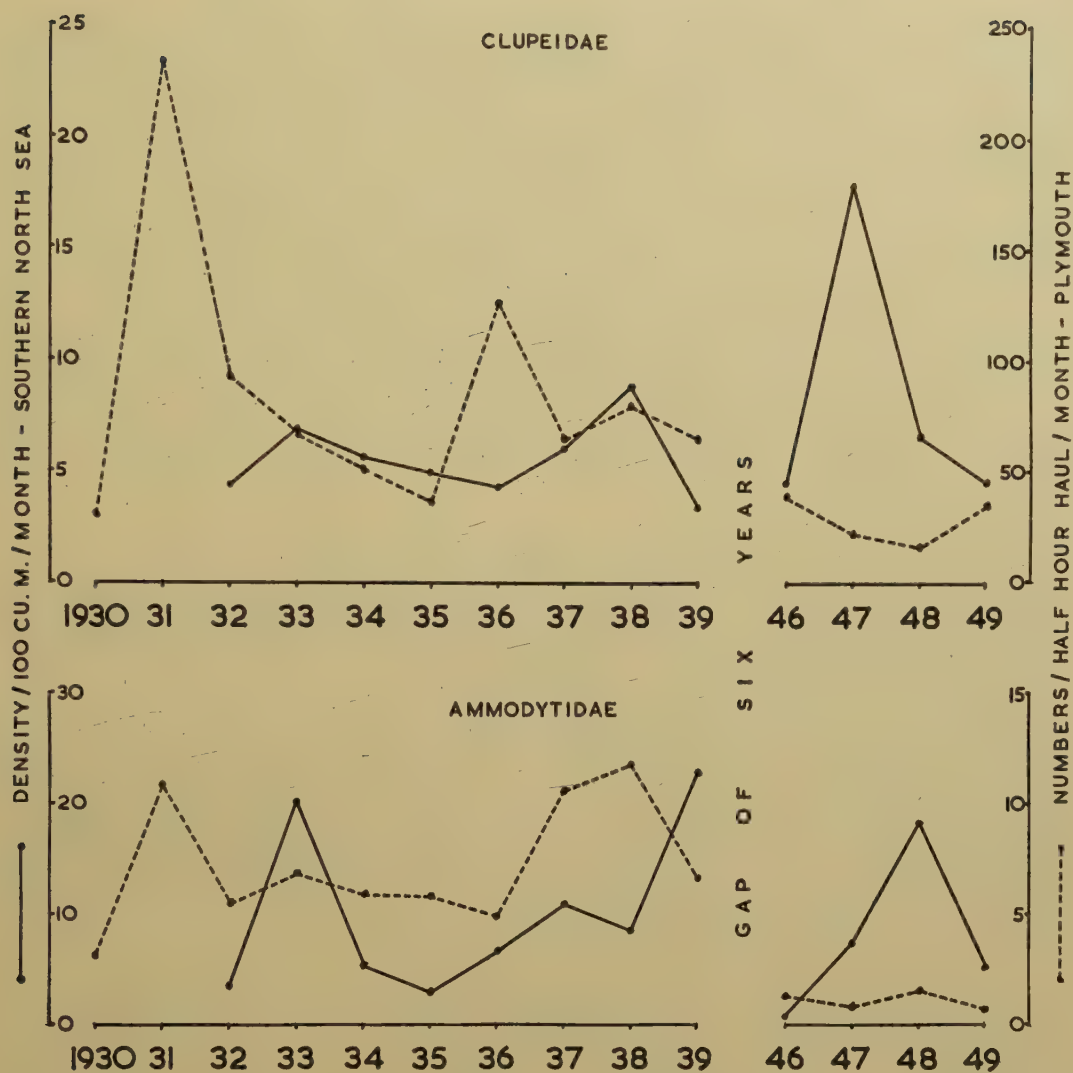
were in 1939. (It is important to note that in both areas the sampling in 1946 was incomplete.) A declining trend in both areas might have been expected for a time, as the stocks would have accumulated during the close period, and then have been diminished progressively as fishing operations were resumed. Taking the catch per unit effort of fishing as an indication of this, there was a decline in yield in both areas from about two or three times the pre-war level in 1946 to a level in 1949 which is very close to that of the pre-war years.

This opposition of trends is not evident for either Clupeidae or Ammodytidae, as may be seen in Text-fig. 10, where these two groups are plotted. In both there is a decline from higher levels of 1931-33 to troughs of low productivity about 1934-36, followed by a recovery, in 1937-39, to levels comparable with the initial ones. The peaks and troughs, however, are not synchronous and there is a suggestion of a lag of two years between events in the Channel and those in the southern North Sea which may correspond. In the post-war period, with limited sampling in 1946, there has hardly been sufficient time to reveal any such correspondence, although the relatively large numbers for the southern North Sea are more evident than in the pre-war period.

The actual densities of young fish of the combined group present some marked differences in the two areas. The figures for the southern North Sea are expressed as numbers per 100 cu.m. sampled, but the volume filtered per standard half-hour haul in the Channel is stated to be 4000 cubic metres. Yet the lowest density of total young fish, excluding Clupeidae and Ammodytidae, for the southern North Sea is 13 per 100 cu.m. in 1932 (omitting the figure for 1946) in comparison with the highest for the Channel of 5.2 per 100 cu.m. in 1930, and in 1939 the North Sea figure is 100 times greater than that for the Channel (50.0 and 0.5). The densities of Clupeidae differ much less, as the range in the southern North Sea is from 4.0 to 18.0 per 100 cu.m. against 0.75 to 6.0 per 100 cu.m. in the Channel. On the other hand, the Ammodytidae show much greater differences between the two areas, the range of density in the North Sea being from 1.0 to 22.0 per 100 cu.m., while in the Channel it does not exceed 0.3 per 100 cu.m. The question which arises immediately is whether these pronounced differences in numbers of larvae are real, or result from the different methods employed to furnish the two estimates.

It seems unlikely, from the relevant data available, that the explanation can be found in the differences between oblique and horizontal sampling. The vertical distribution shown by Russell (1928, Table III) suggests that the number of young fish caught at 10 metres would be somewhat less than the average of the numbers caught at the other depths. Thus the differences already noted would, if anything, have been exaggerated if a comparison between catches at 10 metres only had been possible.

A more likely source of bias may lie in the possibility of a relatively high proportion of young fish being capable of avoiding a slow-moving net, especially in daylight. All the Channel samples were taken in daylight, which enhances their value for comparison *inter se*, but leaves open the possibility that there was some



TEXT-FIG. 10.—Graphs comparing fluctuations in numbers of young Clupeidae and Ammodytidae taken by the recorder in the southern Northern Sea (solid line) and in tow-nettings at a point in the English Channel off Plymouth (broken line) for the years 1932–39 and 1946–49. The figures for 1946 are based on limited sampling in both areas.

reduction in the catch, due to such “avoidance,” in that part of the haul taken in the upper illuminated layers.<sup>1</sup>

The Plankton Recorder has a much greater speed of advance, of from 8 to 12 knots, so that in spite of its relatively small aperture the chance of young fish

<sup>1</sup> Mr. Bridger (private communication) has shown through a reassessment of earlier published work that comparatively few young fish were taken by vertical net hauls during the day in the southern North Sea. His conclusion, that this was due to the larvae avoiding capture rather than to their vertical distribution, is largely confirmed by his recent experiments with high speed samplers.



darting out of its path is correspondingly less. It may also be significant that unlike the net the recorder has no towing wire or bridles in front of its aperture to create a disturbance in the water and so give advance warning of its approach. The recorder tows were spread fairly evenly over day and night, but there is no evidence that the numbers taken at 10 metres differed in this area according to whether they were caught during daylight or in darkness. The relative numbers caught do not appear to have been influenced by diurnal migration or by avoidance of the gear in daylight.

It is just possible that the station 2 miles east of the Eddystone Lighthouse is so situated in the Channel that it supports an atypically low population of young fish. Parts of the southern North Sea traversed by the recorder routes can be selected to show population levels quite as low as those found in the Channel, but here the low numbers have been found consistently, and are characteristic of such areas. None have been noted as showing a decline in numbers similar to that seen in the Channel results.

However, none of the differences arising out of different sampling techniques can account for the reciprocal trends in the populations of young fish in the two areas. The techniques have been consistent in both cases, and the trends shown in Text-fig. 9 can thus be accepted as reflecting opposed tendencies in the two areas. Russell (1939, 1940) attributed the decline in numbers of young fish in the Channel to changes in the environment brought about by a progressive reduction in the amount of "Atlantic" water entering the Channel. This explanation is supported by the culturing experiments of Wilson (1951, 1952) who finds that water from the Channel is now a less successful medium for his test species than water from the Celtic Sea or the Clyde. The possibility that the increase in the numbers of young fish in the southern North Sea may have been caused by a similar, but favourable, gross change in conditions is an interesting speculation.

#### SUMMARY.

1. The young fish and fish eggs were collected, from the standard depth of 10 metres, in the course of the Continuous Plankton Recorder survey of the North Sea and adjacent waters during the years 1932-39 and 1946-49.

2. The distributions of young fish and of fish eggs in the North Sea are described. Average distributions for the total fish eggs and several groups of young fish, based on the results from all the years over which the survey extended, are shown for the important months in the year. The patterns of distribution found show that for most groups the "spring" period is one of concentration mainly in the southern and south-eastern parts of the area, while in the "summer" period the central and northern parts of the area were more densely populated. These patterns of distribution are repeated with marked regularity in the individual years, the variations in locus and extent from year to year being of relatively small magnitude. The

identity of the fish eggs, which depends largely on circumstantial evidence, is suggested and discussed, and the specific composition of the groups containing pleuronectids and gadoids, based on the occurrences of large numbers, and the regular recurrences of small numbers, is indicated and related to other results obtained in the area.

3. The results from the Atlantic routes for the years 1948 and 1949 are outlined, and the sampling of separate populations is shown. The shallower inshore ends of these routes show results very similar to those found for the North Sea, but the "summer" maximum in the number of fish eggs falls in May, a month earlier than in the North Sea. The offshore portions of these routes, lying over the deeper water outside the Continental shelf, are characterized by small numbers of fish eggs, and by relatively few young fish except for the patches of *Gadus poutassou* found in April, which are shown. In June and August there is a general, but scattered, occurrence of deep water species.

4. The seasonal changes in abundance in the North Sea of the various groups of young fish, and of the fish eggs, are shown, and the differences between different parts of the area are discussed. In the southern North Sea, sampled from 1932, there is a build up of numbers of all groups except clupeids from January to March, which forms a "spring" peak. In April and May numbers are low, but a "summer" peak is found in June and July, which has died down by August. For the rest of the year the numbers are negligible. The fish eggs follow this sequence of events in all parts of the North Sea, suggestive of the existence of two quite clearly defined periods of spawning activity. The sequences in the other groups of young fish are generally similar in the north-western area of the North Sea, but there are some differences in the north-eastern area. These seasonal variations are clearly evident in each individual year, and may be regarded as typical.

5. The fluctuations in abundance from year to year of the fish eggs and the several groups of young fish are stated and discussed. In the southern North Sea the fish eggs show a decline in mean density from 1932 to the 1935-37 period, with a recovery in 1938 and 1939 to a level rather above that of 1932. In the groups containing the pleuronectid and gadoid larvae there is a generally rising trend in the figures for the years from 1932 to 1939, with very high figures in 1939. The numbers of Clupeidae and Ammodytidae, however, decline from 1933 to 1936 and 1935, then recover to about the original levels in 1938 and 1939 respectively. In the post-war years there is a fall in numbers from very high levels in 1946 to about the average level in 1949 in most cases except for *Scomber scombrus*, where there is an increase of roughly similar proportions. The trends are generally similar in the north-western and north-eastern areas of the North Sea as far as the records extend.

6. Throughout the whole period of the survey there is a marked similarity between the curve expressing the annual fluctuations in the number of fish eggs recorded and that showing the contemporary fluctuations in yield of total demersal fish per unit effort of fishing.



7. The results from the southern North Sea, for total young fish excluding Clupeidae and Ammodytidae, and for these latter separately, are compared with those found in the Channel over the same period. A higher density of young fish appears to be found in the North Sea than in the Channel, and some possible reasons for such differences are discussed. The trends of the average populations in the two areas are, however, markedly opposed up to 1939, that in the Channel declining while that in the North Sea increased. From 1946 to 1949 the numbers in both areas are decreasing, but in the North Sea in 1949 the numbers are still about the average level whereas in the Channel they have fallen to a very low level.

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## EXPLANATION OF PLATES XX-XXVII.

Plates XX to XXVII comprise series of charts showing the distribution of fish eggs and various groups of young fish on the recorder routes in the North Sea during certain selected months. The symbols represent the average numbers taken on each 10-mile block over a period of years, from 1938 to 1939 and 1946 to 1949 in the northern part of the area, but with the addition of the years 1932 to 1937 in the southern part; for further details see p. 219 and Text-fig. 5. Letters placed against symbols indicate the species most commonly found in that sample.

### PLATE XX.

Charts showing the distribution of the total fish eggs during the months January to June. The letters which indicate the commoner species are based partly on the identification of eggs and partly on circumstantial evidence derived from associated larvae. (For July and August charts and key see Plate XXIV.)

### PLATE XXI.

Charts showing the distribution of the total Clupiedae during the months January to June.

### PLATE XXII.

(In continuation of Plate XXI.) Charts showing the distribution of the total Clupeidae during the months July to December.

### PLATE XXIII.

Charts showing the distribution of the total Ammodytidae during the months January to June (For July to September charts see Plate XXIV.)

### PLATE XXIV.

(In continuation of Plates XX and XXIII.) Charts showing the distribution of the total Ammodytidae during the months July to September, and that of the fish eggs for the months July and August.

### PLATE XXV.

Charts showing the distribution of the total Pleuronectidae during the months January to June. The letters indicate the positions at which certain species have occurred frequently or in large numbers. (For July and August charts and key see Plate XXVII.)

### PLATE XXVI.

Charts showing the distribution of the total Gadidae during the months January to June. The letters indicating species are based on the frequent recurrence, or the occurrence in large numbers, of some of the species of food fishes. (For July and August charts and key see Plate XXVII.) The symbol  $\triangle$  is used on some of these charts to indicate the presence of a species which was found in numbers below the value of the lowest symbol.

### PLATE XXVII.

(In continuation of Plates XXV and XXVI.) Charts showing the distribution of the total Pleuronectidae and the total Gadidae during the months of July and August.

